CHARACTERIZATION OF THE PLANKTON COMMUNITY IN THE LOWER RINCON DELTA: INVESTIGATIONS REGARDING NEW APPROACHES TO MANAGEMENT

A Dissertation

by

YESIM BUYUKATES

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2003

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

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ABSTRACT

Characterization of the Plankton Community in the Lower Rincon Delta: Investigations Regarding New Approaches to Management. (December 2003)

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Chair of Advisory Committee: Dr. Daniel L. Roelke

In light of increasing harmful algal blooms and the need to protect human health and aquatic resources, proactive management approaches merit further study. For this purpose I conducted field samplings to characterize plankton community composition and laboratory experiments to test some approaches to new management schemes in the lower Rincon Delta. On site measurements and microscopic analysis showed that environmental parameters and plankton community composition varied considerably among sampling stations and sampling dates. A recent modeling study suggested that manipulation of freshwater inflow to estuaries might prevent phytoplankton blooms and enhance secondary productivity. To test this theory I conducted three semi-continuous design and flow-through incubation design experiments using natural plankton assemblages. I investigated the effect of two different pulsing regimes of inflow and nutrient loading on zooplankton densities, and phytoplankton biomass and diversity. Despite differences in zooplankton structure and phytoplankton community composition between the two experiment designs, the results confirmed that pulsed inflows might

alter plankton dynamics. My findings showed that 3-day pulse treatments consistently supported greater zooplankton densities and higher phytoplankton species diversity when compared to 1-day pulse treatments. In addition, accumulation of phytoplankton biovolume remained low during 3-day pulse treatments. Differences in zooplankton performance between 3-day pulse and 1-day pulse inflow treatments were likely due to the ability of phytoplankton to uptake and store greater amounts of nutrients under conditions of 3-day pulse inflow. This resulted in food of higher quality for zooplankton, and might have supported greater zooplankton population growth rates. Additionally, in an attempt to understand the mechanisms leading to high biodiversity in aquatic ecosystems, I built a resource-storage model and studied the effects of resource-storage on competition of multiple phytoplankton species on multiple abiotic resources. I compared this model with a well-established multi-species competition model. My results showed that for certain species combinations a resource-storage-based model can generate dissimilar outcomes when compared to a model without resource-storage.

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CHAPTER I

INTRODUCTION

The development of successful management schemes in coastal systems greatly relies on understanding the processes affecting succession within the plankton, as well as the initial composition of the plankton community. With this knowledge, it may be possible to predict the changes in phytoplankton community composition that result from natural and/or controlled perturbations. However, to perform such a prediction with any accuracy, the relationships between phytoplankton growth and their physical and biological environments must be understood. Components of the physical environment that affect the growth and community structure of phytoplankton are many and diverse, and they include nutrient availability, light intensity, water movement and salinity (Smayda 1980; Reynolds 1989; Lehman and Smith 1991). Similarly, components of the biological environment that influence phytoplankton succession include selective predation/grazing pressure, and negative interactions between organisms such as phytoplankton, bacteria and zooplankton (Margalef 1958; Smayda 1980; Doucette 1995; Doucette et al. 1999). Because aquatic systems are dynamic in nature and can be affected diversely by various fluctuations, survival and development of organisms require that the system in question be of sufficient quality to sustain the different components. Therefore, a thorough knowledge of the system and the processes affecting the system are required.

This dissertation follows the style of Limnology and Oceanography.

The overarching objective of this study was to obtain insight into the spatial and temporal variability of plankton community structure and how it responded to pulse vs. continuous nutrient perturbations in the study system, a tidal creek of Rincon Delta, Corpus Christi, Texas.

After a brief description of the system and some of the system parameters in Chapter II, the dissertation is organized as follows. Chapter III provides experimental support to a recent modeling study, that suggests episodic inflow and nutrient loading events might result in greater secondary productivity and less accumulated phytoplankton biomass when compared to inflows that are more continuous. For this purpose I conducted microcosm experiments which implemented semi-continuous design of 1- and 3-day nutrient pulses on natural plankton assemblage from the system. In chapter IV, I evaluate how the differing zooplankton community structure influenced the role of pulsed inflows on phytoplankton species diversity and secondary productivity and compare succession patterns between the two types of experiments, semi-continuous and flow-through designs. Mechanisms effecting zooplankton and phytoplankton structure are myriad and interactions are complex, but episodic inflow and nutrient loading events can alter succession patterns in a predictable fashion. In an attempt to understand the mechanisms that impact biodiversity, Chapter V tries to answer the question “How can competing species coexist?” by using an untraditional method, the chaotic behavior of nonlinear system dynamics. In this chapter I compare a well-established multi-species competition model with a more complex model that is believed to be a better representation of the natural system.

CHAPTER II

SYSTEM CHARACTERISTICS

Introduction

A thorough knowledge of an aquatic system is paramount to understand the individual and/or mutual effects of physical and biological environments on the plankton community composition.

Rincon Delta (Corpus Christi, Texas) is a bird sanctuary and a regulated wetland with vegetated marshes, mudflats and open water (Fig. 1). It covers approximately 75 km^2 (Bureau of Reclamation 2000). Other dominant features of the study site include the lower Nueces River, which encompasses a discharge site for the Corpus Christi Allison Sewage Treatment Plant (STP) and an area of heavy industry dominated by oil refineries (Buyukates and Roelke 2000). The lower Rincon Delta is dominated by brackish and saltwater marshes. The system is shallow with a maximum depth of 1.2 m and it is completely mixed through the water column. Salinity varies with river inflow from Calallen Gauge, weak tidal exchange, precipitation and wind-driven water exchange with the bay. Phytoplankton primary production is controlled by N availability throughout the year (Roelke et al. 1997; Bureau of Reclamation 2000).

Fundamental understanding of the system depends on the freshwater requirements of the region, which consists of two elements: the wetland and the region's industry. Freshwater input to the wetland is important to maintain the environmental health of the marsh ecosystem since it supplies the nutrients that are necessary for the

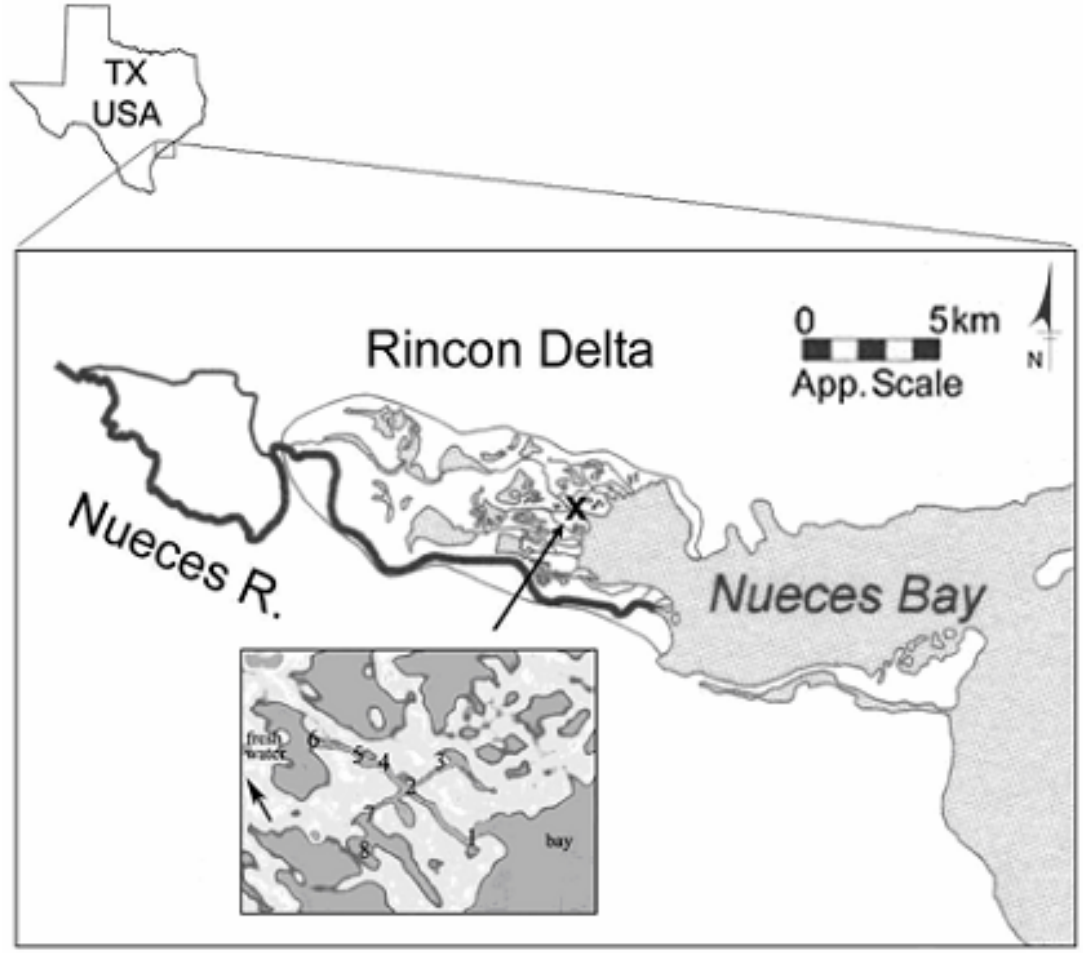

Fig. 1. The Nueces River and Bay, and the Rincon Delta. The delta is a bird sanctuary and a regulated wetland with vegetated marshes, mudflats and open water. The system is shallow with a maximum depth of 1.2 m (from Bureau of Reclamation 2000). Water samples for the laboratory experiments were collected from station 2 (27°52' N; 97°31' W).

growth and development of phytoplankton. Lack of freshwater input (extended drought conditions) may cause hypersalinity, which can affect the osmotic concentration of the seawater, relative proportion of solutes within the estuarine water, concentration of dissolved gasses, and density and viscosity of water, which in turn impacts the phytoplankton in the system. Additionally, in summer, when the water temperature increases and the water flow is reduced, organic matter degradation by bacteria and other microorganisms can cause an increase in oxygen consumption. Consequently, low oxygen, or even anoxia may lead to increased gaseous hydrogen sulfide (H_2S) production removing available iron (Fe) and sulfur (SO_4) from the system. This may cause the limitation of these nutrients, which may have negative impacts on the growth of different phytoplankton species (Horne and Goldman 1994). In addition H_2S is toxic to aerobes (Horne and Goldman 1994). Given the above information, the reduction of freshwater flow to the system can alter the production of phytoplankton in various ways, also affecting the production of higher trophic levels that use phytoplankton as a food source.

One of the potential problems that causes reduction of freshwater inflow to the Rincon Delta is increasing water demand by the petroleum industry, especially as used in cooling towers. As water is lost to evaporation, the cooling towers constantly add water to their system to compensate. Although it differs with the cooling tower's size, pumps generally supply water at over 100,000 gallons/min to one or more cooling towers. This tremendous freshwater requirement by the industry brings forth the

question, “How is the productivity of the delta affected due to reduced freshwater inflow?”

As demand for water from industry increases, the amount of water available to meet the needs of the marsh ecosystem decreases. Faced with this problem, one of the concerns of the city of Corpus Christi is the reduction of productivity due to reduced freshwater inflow. The potential solution considered by the city of Corpus Christi is the cessation of freshwater flow from the river to the Rincon Delta and replacement of freshwater flow with the discharge from nearby sewage treatment plants. The obvious concern with this scheme is the impact that the increased nutrient loading will have on the plankton dynamics of the Rincon Delta.

Materials and methods

Field samplings were performed to gather information on the plankton community of a tidal creek of Rincon Delta. This was used to determine the initial community composition for the experiments in Chapters III and IV. Two end members (freshwater and saltwater) and 8 stations are assigned for sampling through one of the creeks of Rincon Delta. Water samples were collected from each station for nutrient, chlorophyll a (chl a) analyses, as well as phytoplankton and zooplankton enumeration on 15 March, 7 June and 8 September, 2001. Environmental parameters were measured on site at the time of sampling.

The amount of nutrients available for phytoplankton is an important factor shaping the composition of the phytoplankton. Therefore, water samples (100 ml) were

collected from the surface and filtered through 47-mm Whatman GF/F glass fiber filters at the site to analyze inorganic nutrients. Samples were kept frozen until analyses. Analyses of inorganic nutrients such as nitrate (NO_3), ammonium (NH_4) and nitrite (NO_2) which form the dissolved inorganic nitrogen (DIN) pools, and orthophosphate (PO_4) and silicate (SiO_3) were conducted using an automated continuous flow analyzer (Grasshoff et al. 1983).

Chl a is an index of biomass. Thus, chl a was analyzed with a model 10-AU Turner Designs fluorometer after extraction by 90% acetone (Arar and Collins 1992). Filters that were used for filtration of surface water for the nutrient analysis were wrapped in aluminum foil and kept frozen until analysis.

The phytoplankton groups in the system were enumerated to the genus level and zooplankton was enumerated to major taxonomic groups, i.e., adult copepods, nauplii, rotifers, and protozoans. Whole water phytoplankton samples were collected as well as net samples using a 20µm mesh size phytoplankton net. Zooplankton samples were collected using a Schindler trap having a 63µm mesh size cod end. Phytoplankton samples were preserved with glutaraldehyde (5% by volume), and zooplankton samples were preserved with formaldehyde (10% by volume). Inverted microscopy was used to enumerate both zooplankton and phytoplankton samples. Details of the microscopic analysis will be detailed in the following chapters. Phytoplankton species diversity was determined using the Shannon-Weaver index (Shannon and Weaver 1949),

$$H' = \sum_{i=1}^{n} p_i \log_2(p_i) \qquad (1)$$

where p_i was the proportion of biomass for species i relative to the total biomass at a specific time.

Environmental parameters have direct and/or indirect effects on the plankton community composition of the system. Therefore, pH, temperature, dissolved oxygen, redox potential, and salinity were measured from surface water using a Hydrolab H20 Water Quality Multiprobe.

An estimation of flushing rate and residence time was necessary because they directly affect nutrient availability, thus affecting phytoplankton development. In the laboratory experiments, these values were meant to resemble post-management conditions in the Rincon Delta after diversion of effluent from a nearby sewage treatment plant into the target tidal creek. Therefore, values for flushing rate and periodicity, as well as nutrient loading magnitude and ratio (for nitrogen and phosphorus only) were selected according to previous studies (Roelke et al. 1997; Roelke 2000).

In the case of diversion of effluent from a nearby sewage treatment plant into the target tidal creek, flushing rate and residence time was determined using the following equations:

$$F_{est}\ (L\ d^{-1}) = \left(\frac{S_{sw}}{S_{sw} - S_{est}} \right) \times F_{fr} \tag{2}$$

$$F_{sw}\ (L\ d^{-1}) = F_{est} - F_{fr} \tag{3}$$

$$\text{Residence time}\ (d^{-1}) = \left(\frac{\text{flow rate}}{V_{est}} \right) \tag{4}$$

where F_{est} was the flow of the estuary, S_{sw} was the salinity of the seawater, S_{est} was the salinity of the estuary, F_{fr} was the freshwater flow and V_{est} was the volume of the estuary (depth×length×width) (Roelke et al. 1997). Note that evaporation was not included in the equations. Previous measurements of freshwater flow data from Roelke et al. (1997) were used in the equations. Horizontal dimensions of the tidal creek were determined with aerial photography (Earth Research System, USGS). Depth of the tidal creek was measured during the sampling trips. These measurements were used to determine the volume of the estuary.

Results

Analyses showed that Si concentrations were always high in the system, NO_3-nitrogen was the main source of the DIN and nitrogen was the limiting nutrient for the primary production (Table 1). In all samplings chl a maximum coincided with the phytoplankton concentration maximum (Fig. 2).

In March and September, diatoms and green algae dominated the phytoplankton while in June diatoms and dinoflagellates were the dominant groups (Fig. 2). Diatoms were dominated by pennates, specifically *Nitzschia* and *Navicula* species, at all times. Additionally small centric diatoms were abundant in September. Composition of green algae changed considerably depending on the season. Coccoid and oblong forms were dominant in March and June while *Crucigenia*, *Scenedesmus*, *Tetraedron* and *Tetrastrum* species dominated the green algae in September. *Cryptomonad* sp. was also present in September. *Peridinium* and some other forms dominated the dinoflagellates

while coccoid forms dominated the cyanobacteria. Both abundance and composition of phytoplankton varied considerably between the stations (Fig. 2). Finally, phytoplankton species diversity was higher in September when compared to March and June (Fig. 3).

Similarly, zooplankton composition and abundance showed high spatial variability (Fig. 4). Adult copepods and rotifers were more abundant in September when compared to March and June.

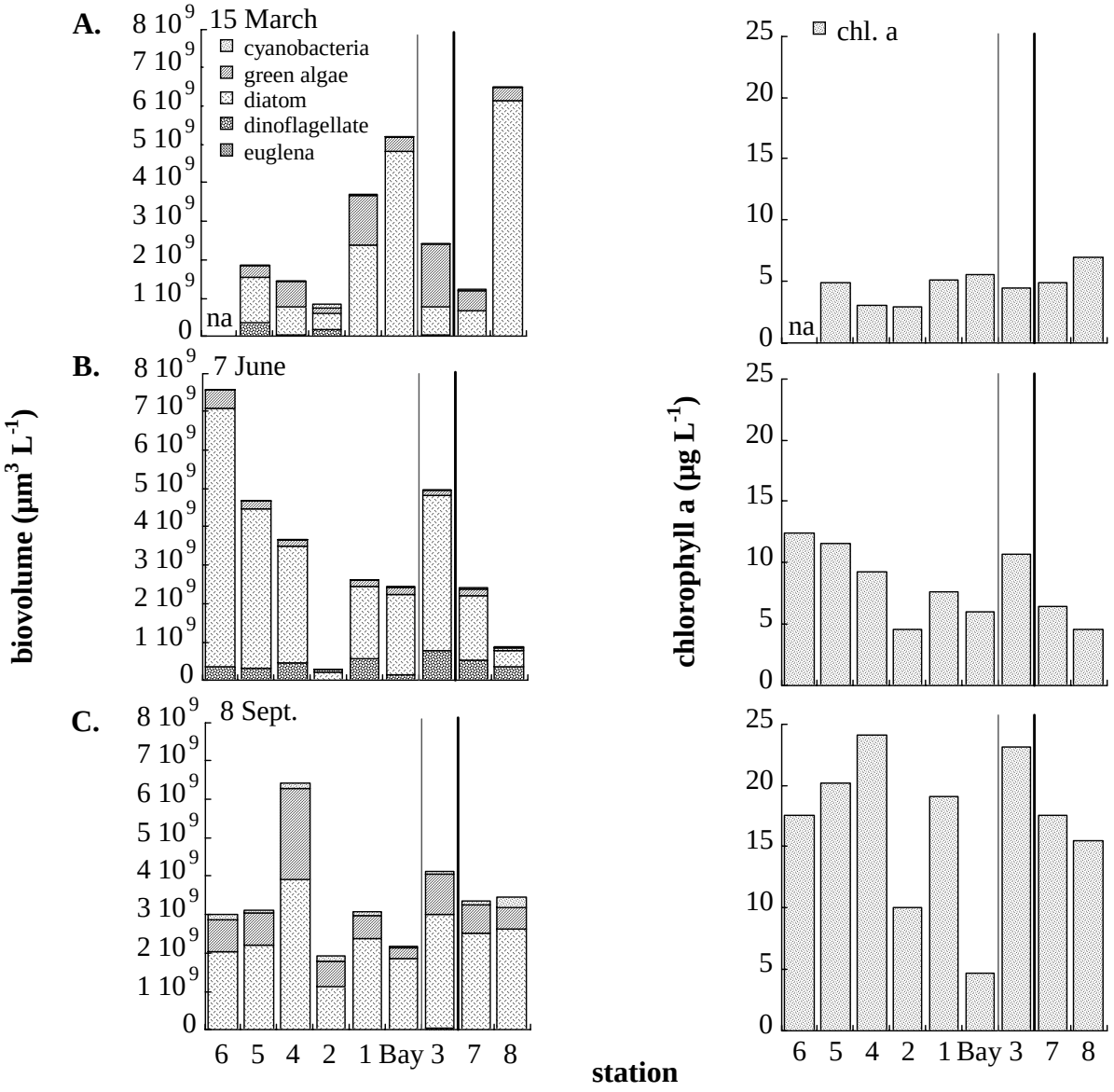

Fig. 2. Phytoplankton and chlorophyll a concentration for (A) March, (B) June and (C) September sampling. Data were not available for station 6 in March. Note that station 2 represented the water collection site for the laboratory experiments. The thin and thick vertical lines separate the stations that were in the pool areas (Fig.1. st. 3, 7, 8) from the others.

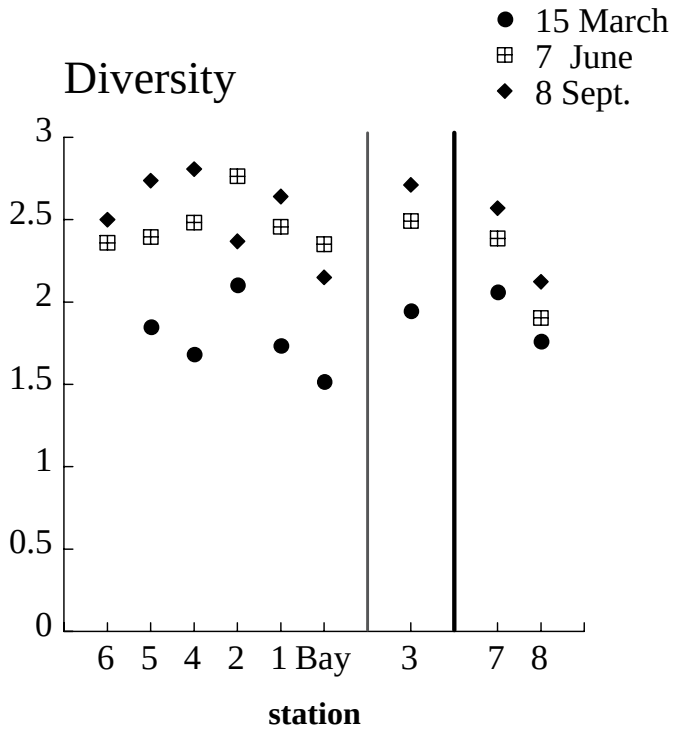

Fig. 3. Phytoplankton species diversity for March, June and September sampling. Data were not available for station 6 in March. Note that station 2 represented the water collection site for the laboratory experiments. The thin and thick vertical lines separate the stations that were in the pool areas (Fig.1. st. 3, 7, 8) from the others.

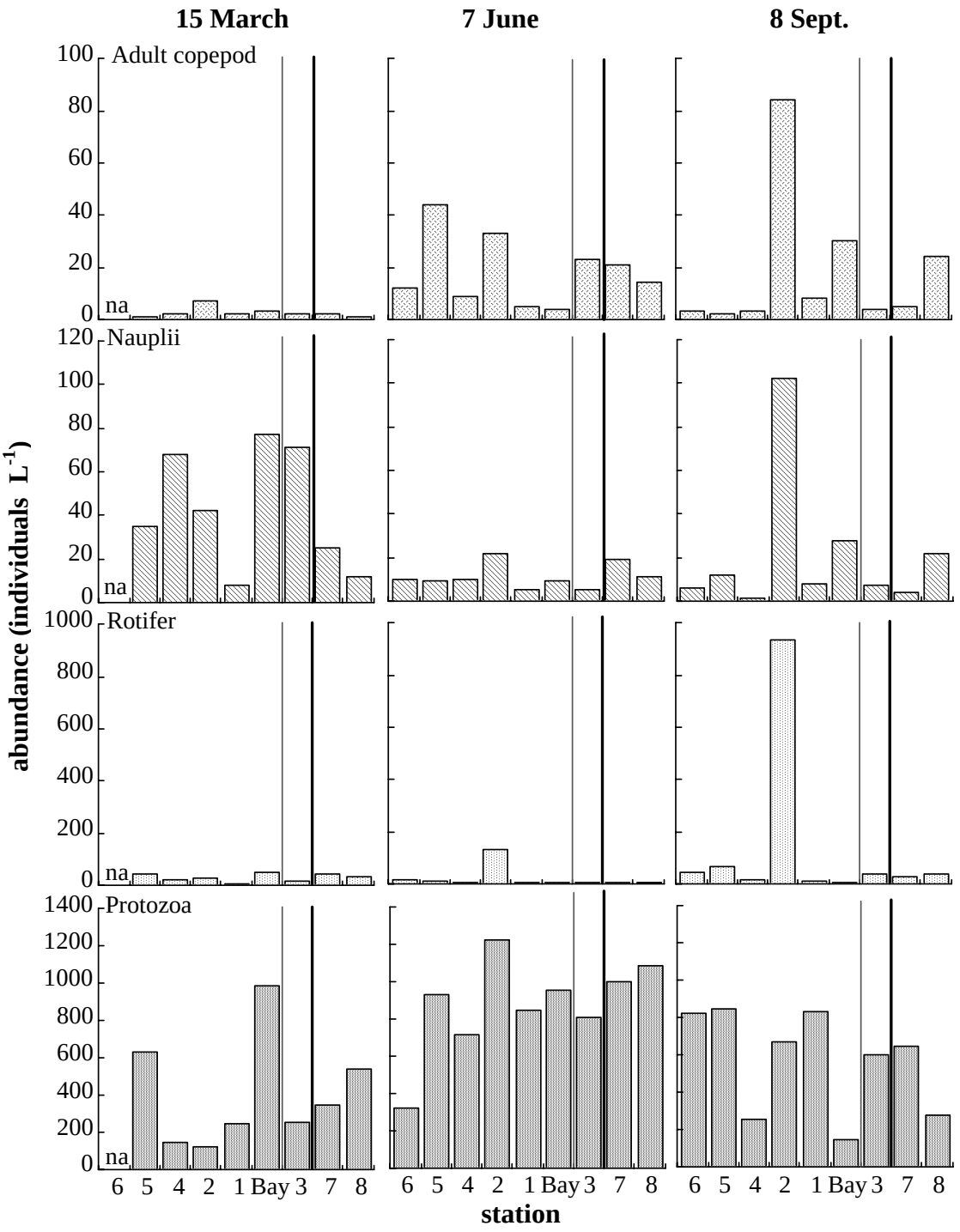

Fig. 4. Adult copepod , nauplii, rotifer and protozoa abundance for March, June and September sampling. Data were not available for station 6. Note that station 2 represented the water collection site for the laboratory experiments. The thin and thick vertical lines separate the stations that were in the pool areas (Fig.1. st. 3, 7, 8) from the others.

Table 1. Concentrations of dissolved inorganic nutrients (μmol L^{-1}) from each station on 15 March, 7 June and 8 September, 2001. DIN = NO_3 + NO_2 + NH_4; nd : under detection limits; na : not able to sample; bold : data from the water collection site for the experiments.

Date	Sta.	NO_3	NO_2	NH_4	Urea	PO_4	SiO_3	DIN	DIN/PO_4
15 March	6	na	na	na	na	na	na	na	na
	5	0.41	0.02	nd	1.09	0.50	46.62	0.43	0.86
	4	0.52	0.05	nd	1.27	0.56	47.00	0.57	1.02
	2	**0.56**	**0.10**	**nd**	**1.39**	**1.45**	**47.30**	**0.66**	**0.46**
	1	0.59	0.12	nd	0.88	2.21	47.04	0.71	0.32
	Bay	0.96	0.15	0.06	0.66	1.18	46.84	1.17	0.99
	River	0.12	0.15	0.37	0.98	4.42	44.84	0.64	0.14
	3	0.39	0.06	nd	0.90	1.26	46.04	0.45	0.36
	7	0.35	0.10	nd	0.98	1.49	46.52	0.45	0.30
	8	0.48	0.13	nd	1.02	3.40	47.20	0.61	0.18
7 June	6	1.21	0.07	nd	0.72	1.28	195.86	1.28	1.00
	5	1.19	0.09	nd	0.72	1.26	202.40	1.28	1.02
	4	1.23	0.09	nd	1.33	1.27	224.22	1.32	1.04
	2	**1.20**	**0.16**	**nd**	**0.44**	**2.59**	**140.39**	**1.36**	**0.52**
	1	0.99	0.09	0.03	0.79	1.75	144.62	1.11	0.63
	Bay	1.14	0.03	0.11	0.85	1.10	115.58	1.28	1.16
	River	1.27	0.03	0.16	0.46	1.31	345.25	1.46	1.11
	3	1.13	0.05	0.02	0.44	1.77	138.50	1.20	0.68
	7	1.37	0.05	0.08	0.62	1.37	125.13	1.50	1.09
	8	1.64	0.06	0.08	1.80	1.48	130.12	1.78	1.20
8 Sept.	6	0.98	0.20	0.58	3.23	14.86	319.69	1.76	0.12
	5	0.94	0.17	0.56	2.85	14.68	308.51	1.67	0.11
	4	0.97	0.23	0.62	3.57	15.22	321.13	1.82	0.12
	2	**0.94**	**0.18**	**0.61**	**2.95**	**15.22**	**333.38**	**1.73**	**0.11**
	1	1.49	0.22	0.61	2.97	9.14	278.20	2.32	0.25
	Bay	1.58	0.48	1.33	2.55	5.74	232.74	3.39	0.59
	River	14.48	1.02	2.07	2.24	7.98	437.64	17.57	2.20
	3	0.92	0.22	0.58	3.04	13.39	334.48	1.72	0.13
	7	0.98	0.16	0.54	2.66	12.68	315.36	1.68	0.13
	8	0.98	0.18	0.50	2.49	11.11	297.46	1.66	0.15

Salinity and water temperature varied considerably among sampling dates. During March and June samplings, temperature was 19.0ºC and 28.4ºC, and the salinity was 37 psu. and 41 psu. at the water collection site for the laboratory experiments, respectively. During September sampling, the salinity was 5 psu. due to recent rain and flooding, and the temperature was 27ºC (Table 2). After the calculations, residence time of the system was found to be 0.11 d^{-1} and this was used to calculate the flow to and from the system in the experimental designs which were detailed in Chapters III and IV.

Discussion

Field data showed spatial variability among sampling dates. Although Si concentration was always high in the system, import of new Si due to heavy rain events caused a dramatic increase in Si concentration in September. This is because unlike other nutrients the main source of Si to an aquatic system is via weathering of silicate bearing rocks through runoff (Horne and Goldman 1994). N concentration was low and DIN:P was much less than Redfield stoichiometry throughout the stations in all sampling times. Similarly, N and P concentrations increased due to heavy rainfall and flooding events in September.

The study system was nitrogen-limited and phosphorus sufficient at the time of sampling in March and June. This favored some k-selected species. These included *Anabaena* spp., *Peridinium* spp., and *Euglena sp.* Representatives from these genera are typically slower growing and less edible (Paerl 1988; Pollingher 1988; Reynolds 1988; Sterner and Hessen 1994). As a result of increased freshwater inflows following heavy

Table 2. Environmental parameters from each station on 15 March, 7 June and 8 September, 2001. na : not able to sample due to equipment problems; * : too turbid to sample; – : too shallow to sample; ~ : not measured in that particular station; bold : data from the water collection site for the experiments.

Date	Sta.	Temp. (°C)	pH	ORP (mV)	Diss. O_2 (mg L^{-1})	Turb. (NTU)	Sal. (ppt)	Secchi Depth (m)
15 March	6	–	–	–	–	–	–	–
	5	19	na	na	na	na	37	–
	4	19	na	na	na	na	37	–
	2	**19**	**na**	**na**	**na**	**na**	**37**	**0.29**
	1	20	na	na	na	na	32	0.63
	Bay	21	na	na	na	na	29	0.31
	River	19	na	na	na	na	0	~
	3	17	na	na	na	na	37	0.43
	7	19	na	na	na	na	37	–
	8	19	na	na	na	na	37	–
7 June	6	32.5	8.24	226	6.89	*	47	0.18
	5	31.7	8.21	219	6.28	*	47	0.18
	4	30.9	8.17	223	5.84	*	47	0.19
	2	**28.4**	**8.05**	**224**	**5.43**	*****	**41**	**0.30**
	1	28.7	8.06	225	5.44	85	41	0.38
	Bay	31.3	8.19	215	7.07	35	37	0.61
	River	29.2	8.17	217	6.18	0	1.07	~
	3	28.8	8.05	221	5.57	*	40	0.26
	7	31.6	8.20	223	6.69	101	37	0.22
	8	32.5	8.17	209	6.54	*	37	0.15
8 Sept.	6	29.9	8.09	156	7.24	118	5	0.19
	5	29.3	8.06	167	6.99	97	5	0.16
	4	29.2	8.03	161	7.08	*	5	0.17
	2	**27.0**	**8.16**	**145**	**7.66**	*****	**5**	**0.20**
	1	27.2	7.80	144	5.68	60	12	0.27
	Bay	30.0	7.90	166	6.98	149	16	0.18
	River	29.8	7.81	265	6.31	0	0.64	~
	3	29.6	8.12	153	7.38	84	8	0.25
	7	28.7	8.06	147	6.41	74	10	0.17
	8	28.7	8.08	147	7.75	98	10	0.14

rains at the time of sampling in September, r-selected species of green algae and diatoms dominated the system. Typically, r-selected species are characteristic of higher maximum growth rates relative to k-selected species (Sommer 1981; Kilham and Kilham 1980; Reynolds 1984).

Numerically, adult copepods and nauplii dominated the macro-zooplankton in March and June. Rotifers were more abundant in September. Copepod adults and nauplii can graze not only on the phytoplankton that is susceptible to rotifer grazing but also on larger phytoplankton species (Reynolds 1984; Sterner 1989). Additionally, previous studies have shown that copepod adults can graze on rotifers, and also protozoa (Sterner 1989; Ingrid et al. 1996). Therefore, grazing by adult copepods may likely contribute to the lower abundance of rotifers and protozoa in March and lower abundance of rotifers in June. As mentioned previously, field sampling was conducted shortly after heavy rain events in September. Low salinity and high nutrient concentration lead to an increase of rapidly-growing and edible phytoplankton forms, which often have smaller cell size and follow favorable nutrient perturbations (Reynolds 1984; Sommer et al. 1986; Roelke et al. 1997). This likely favored rotifers, which reproduce more rapidly than copepods and prefer prey of smaller cell size (Reynolds 1984; Sterner 1989; Horne and Goldman 1994).

The natural plankton community structure in a tidal creek of the Rincon Delta was diverse and community structure changed due to physical processes, i.e., rain events. As will be seen in the following chapters, the initial conditions of the plankton community structure affected the outcome of the laboratory experiments. Therefore knowing the

initial plankton community composition of a system is important while making manipulations that would result in a diverse and productive system.

CHAPTER III

INFLUENCE OF PULSED INFLOWS AND NUTRIENT LOADING ON NATURAL ZOOPLANKTON AND PHYTOPLANKTON ASSEMBLAGES: EXPERIMENTS USING A SEMI-CONTINUOUS DESIGN

Introduction

Environmental disturbances in aquatic systems alter phytoplankton community structure, diversity, and biomass. For example, enhanced phytoplankton species diversity due to pulsed inflows and associated nutrient loading has been observed in modeling studies (Levins 1979; Ebenhöh 1988; Roelke et al. 1999), microcosm experiments (Sommer 1984; Sommer 1986; Gaedeke and Sommer 1986) and field studies (Padisak 1993; Barbiero et al. 1999; Flöder and Sommer 1999; Hambright and Zohary 2000). In theory, this occurs because disturbances over ranges of appropriate frequency and magnitude suppress competitive exclusion, thereby maintaining higher species diversity (Hutchinson 1961; Tilman 1982). Phytoplankton biomass can also be affected in systems where phytoplankton and zooplankton interactions become decoupled. This occurs because phytoplankton are often able to respond more quickly to altered physicochemical conditions than are zooplankton (Reynolds 1984; Sommer et al. 1986; Angeler et al. 2000).

Because disturbances influence phytoplankton community structure, the zooplankton community is also affected. For example, following a favorable disturbance, succession from less-edible, slower growing, k-selected phytoplankton

species to more edible, rapidly growing, r-selected species might occur. In turn, this may stimulate zooplankton growth (Sommer 1981; Reynolds 1984; Sommer et al. 1986; Roelke et al. 1997). Additionally, high phytoplankton species diversity as a result of disturbances of appropriate frequency and magnitude may favor zooplankton forms that have adopted preferential grazing strategies (Reynolds 1984; Reynolds 1989).

Disturbances might affect zooplankton in another way, i.e., through enhanced food-quality. For example, under conditions of pulsed inflow and nutrient loading, some phytoplankton species uptake and store nutrients at a rate greater than their reproductive rate (Ketchum 1939; Droop 1968; Droop 1983). Higher intracellular stores of nutrients that are limiting to zooplankton may result in enhanced secondary productivity. This phenomenon has been demonstrated using modeling studies (Hessen and Bjerkeng 1997; Roelke 2000) and laboratory experiments (Groeger et al. 1991; DeMott et al. 1998; MacKay and Elser 1998).

On the other hand, if disturbances are inconsequential, phytoplankton biomass might approach the carrying capacity of the system, in which case intracellular nutrient stores would be minimized. Under these conditions, previously suitable prey might become unsuitable because of the nutritional mismatch between predator and prey, i.e., food is of poor quality. In this scenario, classical predator-prey theory, where predator abundance increases with increasing food abundance (Lotka 1932), would fail to describe interactions between zooplankton and phytoplankton. In other words, regardless of high food quantity, poor food quality would result in decreased performance of zooplankton populations (Sommer 1992; Sterner and Hessen 1994; Elser et al. 1998;

Urabe et al. 2002).

These concepts have direct application to watershed management aimed at restoration of coastal wetland and bay systems. For example, the Nueces Delta, TX, not unlike many estuaries of the western Gulf of Mexico, has experienced dramatic declines in freshwater inflow over the past 50 years, which have produced deleterious consequences in the delta (Bureau of Reclamation 2000). Temporary pulsed inflows during a river diversion demonstration project corresponded to dramatic increases in net ecosystem productivity, and improved abundance and diversity of intertidal vegetation and benthic communities (Heilman et al. 1999; Alexander and Dunton 2002; Montagna et al. 2002; Palmer et al. 2002; Ward et al. 2002). It may be that zooplankton populations were also stimulated following mechanisms discussed in the preceding paragraphs, and as predicted in a modeling study of the Nueces River Estuary (Roelke 2000), and observed in other coastal wetlands (Hann and Goldsborough 1997).

I further explored this hypothesis by conducting laboratory experiments on natural plankton assemblages from the Nueces Delta. In these experiments, I focused only on the plankton community with the purpose of testing the model simulations of Roelke (2000), which predicted that pulsed inflows would result in greater accumulation of zooplankton populations, greater phytoplankton species diversity, and less accumulation of phytoplankton biomass. My laboratory experiments were meant only as a proof of concept of the model (Roelke 2000), and not meant to replicate conditions of the natural environment. My experiments are relatively unique, however, because they include natural phytoplankton and zooplankton communities together, thereby allowing

simultaneous direct and indirect interactions between phytoplankton, zooplankton, and the physicochemical environment.

Materials and methods

Three semi-continuous design experiments were performed on 15 March , 7 June and 8 September, 2001 to test the influence of pulsed inflows of varying frequency and magnitude on zooplankton abundance, phytoplankton biovolume, and species diversity. Natural plankton assemblages were collected from surface waters in 20 L Nalgene carboys from the Nueces Delta, Texas (station 2; 27°52' N, 97°31' W). The samples were transported to the laboratory located in College Station, Texas. This process took ~4 h. During this time samples were kept shaded and cool. Prior to the experiment, a portion of the water was filtered through 47 mm Whatman GF/F glass fiber filters. After the filtered water was autoclaved at 121ºC and 15 PSI for 30 min, it was cooled and used in the media preparation. Solid standards were dissolved into the water to prepare the media following an f/2 recipe (Guillard & Ryther 1962), except for nitrogen and phosphorus, which were set according to previous studies (Roelke et al. 1997; Roelke 2000). This process took ~2 h. To avoid bias from large zooplankton a 200 µm mesh-size plankton net was used to pre-filter the water (Sommer 1985), which was then used as inoculum for the experiment. The experiments were started ~6 h after water was collected from the Nueces Delta.

Each of the three experiments was comprised of two treatments, with each treatment performed in triplicate. The treatments were 1-day and 3-day pulsed inflows

where the volume of the chamber was held constant. In other words, plankton were subjected to flushing losses as a function of the media additions. A model I-35LLVL incubator was used in this experiment, which allowed control of temperature, irradiance and photoperiod. The degree of flushing and nutrient loading (for nitrogen and phosphorus only) was calculated using the Eqs. 2, 3, and 4 in the previous chapter. This experimental set-up replicated likely hydraulic and nutrient loading conditions in a target tidal creek in the Nueces Delta should freshwater flow be replaced with discharge from a nearby sewage treatment plant.

The volume of the inoculum was 1 L. The 1-day pulse treatments received a water replacement of 93 ml every day, while the 3-day pulse treatments received a water replacement of 279 ml once every third day. In this way, daily hydraulic residence time was constant at 0.11 d^{-1} for the 1-day pulse treatments, and periodic at 0.33 d^{-1} for the 3-day pulse treatments on days when water was replaced. The 1-day and 3-day treatments received the same magnitude of flushing and nutrient loading over the course of the experiments. The only difference was the frequency and magnitude of the water replacements, or pulses.

Temperature was held constant at 20°C across all treatments, which was the average seasonal temperature in the delta. Similarly, photoperiod was chosen as 12 h. L/D, which was in the photoperiod range of the delta. I used cool white fluorescent bulbs as the light source, and adjusted the irradiance based on light conditions at the field site. Irradiance (I_z) at the time of each sampling was calculated using the following equation, where I_0 was the ambient surface light intensity, k was the extinction coefficient and z

$$I_z = I_o e^{-kz} \quad (5)$$

was the sampling depth. I assumed secchi depth to be one-third of the photic zone and I_z to be defined as 1% of I_0 (Horne and Goldman 1994). Hence k was derived using the formula,

$$k = -\frac{\ln(0.01)}{3 \times \text{secchi depth}} \quad (6)$$

Geometric equations were used to determine the irradiance that accounted for the influence of depth, light attenuation in the water column, latitude, time of day, and time of year (Brock 1981). I assumed complete mixing through the water column, and calculated average irradiance values of 627, 712 and 445 $\mu Em^{-2}s^{-1}$, for the March, June and September samplings, respectively. Depending on the time of day these values change, i.e., low in the morning and evening, and high in the afternoon. To account for this, I chose a lower irradiance of 200 $\mu Em^{-2}s^{-1}$ for the experiments. This value was in the range of typical light saturated photosynthesis rates of many phytoplankton (Kirk 1994).

In each experiment, the water used for the inoculum for each chamber was drawn from the same well-mixed carboy that contained the natural plankton assemblage. Thus, initial phytoplankton and zooplankton community structures were assumed to be very similar in each of the chambers in a given experiment. Chambers were gently swirled twice a day to provide re-suspension of phytoplankton and minimize growth of periphyton, and their position within the incubator was rotated to ensure equal irradiance.

Samples for microscopic analysis were collected at three-day intervals and preserved immediately with 5% glutaraldehyde, v/v. Plankton identification and enumeration were conducted using settling chambers and inverted light microscopy (Utermöhl 1958). Sample volumes of 3 ml for phytoplankton and 5 ml for zooplankton were used. At least 20 random fields of view were counted at 1000×, 400× and 200× magnifications for different cell-size classes of phytoplankton. This resulted in at least 400 individuals counted of each dominant phytoplankton species, and a ± 10 % counting precision within 95 % confidence limit (Lund et al. 1958). The entire settled area was counted for zooplankton. Phytoplankton were identified to the taxonomic level of genus (Prescott 1978). Zooplankton were categorized into copepods (adult, nauplii), rotifers, and protozoa. Phytoplankton cell volumes were estimated by measuring cell dimensions and using common geometric shapes (Wetzel and Likens 1991), and zooplankton sizes were estimated by measuring the length of each individual. Phytoplankton diversity was determined according to Shannon and Weaver (1949).

Differences between pulsed inflows of varying frequency and magnitude were determined using one-way ANOVA tests (SPSS Inc. 1994). In one set of ANOVAs, the dependent variables were the maximum zooplankton population and maximum phytoplankton biovolume that occurred in a chamber. In the other set of ANOVAs, dependent variables were the zooplankton population and phytoplankton biovolume that were integrated over the entire period of experiment. In this way, the second set of ANOVAs accounted for the total performance of zooplankton and phytoplankton

populations over the course of the experiments. Statistically significant differences among treatments was assessed at the 5 % level of confidence.

Results

Periphyton did not accumulate in the chambers for any of the experiments. Therefore, the following results are not compromised due to shading and sequestration of nutrients by periphyton.

Zooplankton abundance in 1-day and 3-day pulse treatments

Zooplankton community structure was different for each of the experiments. Numerically, adult copepods and nauplii dominated the macro-zooplankton in the March and June experiments (Figs. 5, 6) while rotifers were abundant in the September experiment (Fig. 7).

Despite the varying zooplankton community structures, similar responses to the treatments were observed. The maximum and integrated adult copepod and nauplii densities were significantly greater in 3-day pulsed treatments in all experiments (Table 3). The maximum and integrated rotifer densities did not differ among treatments in the March and June experiments, but did show significantly greater densities in the September experiment (Table 3). The maximum and integrated protozoa abundance showed no differential response to variable inflow regime in any of the experiments (Table 3).

In each of the experiments, the size distribution of individuals in the zooplankton categories was indistinguishable between treatments. Therefore, the analysis using

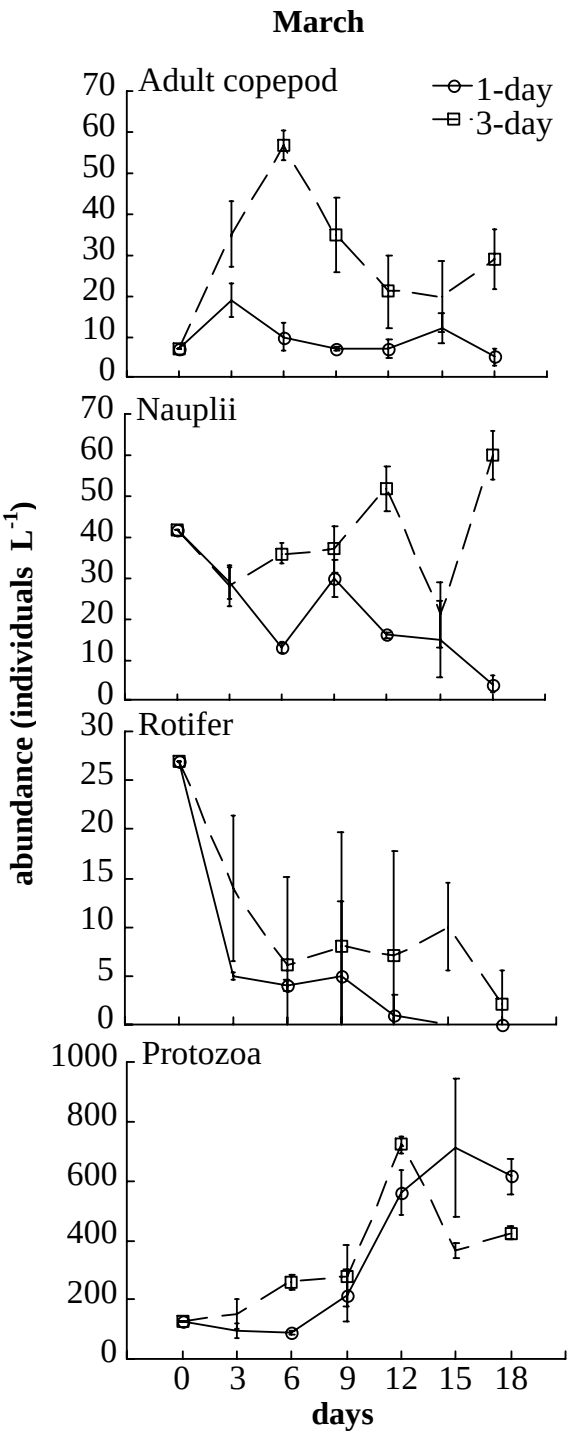

Fig. 5. Changes in adult copepod, nauplii, rotifer and protozoa abundance in 1-day and 3-day pulse treatments in March. Symbols and error bars indicate the mean ± 1 SD for 1-day and 3-day pulse inflow treatments on triplicate chambers.

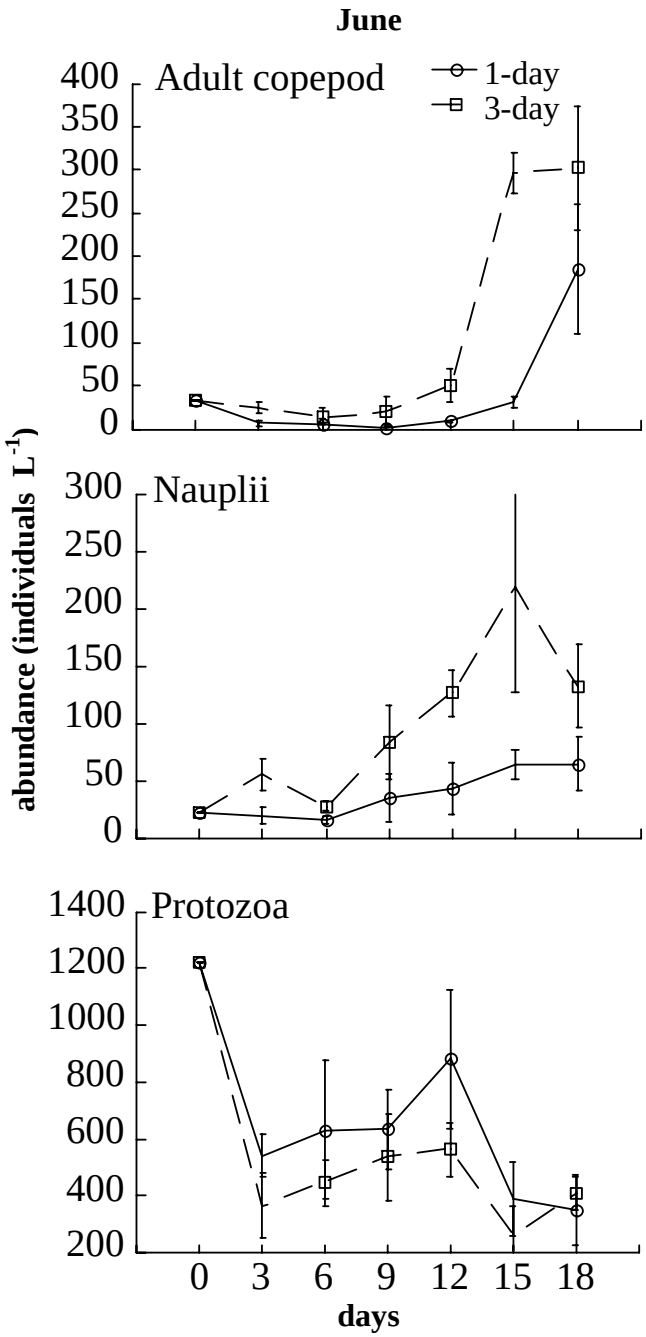

Fig. 6. Changes in adult copepod, nauplii and protozoa abundance in 1-day and 3-day pulse treatments in June. Symbols and error bars indicate the mean ± 1 SD for 1-day and 3-day pulse inflow treatments on triplicate chambers.

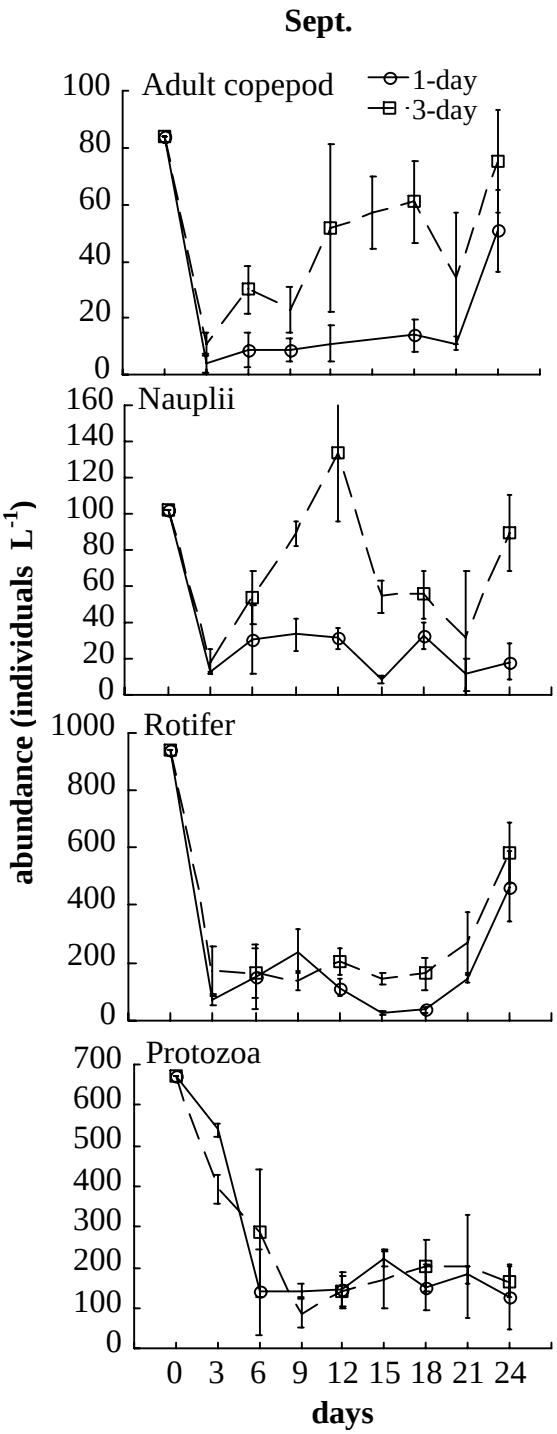

Fig. 7. Changes in adult copepod, nauplii, rotifer and protozoa abundance in 1-day and 3-day pulse treatments in September. Symbols and error bars indicate the mean ± 1 SD for 1-day and 3-day pulse inflow treatments on triplicate chambers.

Table 3. Zooplankton population responses in 1-day vs. 3-day flow treatments for March, June, September experiments. The table lists the experiment, zooplankton groups and results of one-way ANOVA that used variables of maximum zooplankton population (a) and integrated zooplankton population over the entire period of experiment (b) (the mean difference is significant at the .05 level; * = not significant).

Experiment	**Zooplankton groups**	***F(a)*** (max.)	***p(a)*** (max.)	***F(b)*** (integ.)	***p(b)*** (integ.)
March 2001	Adult copepod	25.99	.007	35.50	.004
	Nauplii	14.13	.019	49.54	.002
	Rotifer	2.05	.225*	1.11	.351*
	Protozoa	0.12	.743*	0.11	.748*
June 2001	Adult copepod	9.12	.040	39.78	.003
	Nauplii	8.59	.042	19.05	.012
	Rotifer	n/a	n/a	n/a	n/a
	Protozoa	3.40	.138*	4.49	.101*
Sept. 2001	Adult copepod	11.16	.028	80.14	.001
	Nauplii	25.77	.007	175.11	.000
	Rotifer	12.86	.023	32.98	.004
	Protozoa	1.54	.281*	0.003	.958*

zooplankton population density is reflective of zooplankton population biomass.

Phytoplankton biovolume in 1-day and 3-day pulse treatments

Phytoplankton community structure also varied between experiments (Fig. 8). Initial phytoplankton community was comprised of diatoms, green algae, cyanobacteria, dinoflagellates and euglena in March and June while diatoms, green algae, cyanobacteria and cryptomonads dominated in September. Although cryptomonads were existent in September their contribution to the total phytoplankton biovolume was small. Some genera were found in all three experiments, others were only found in the third experiment. For example, *Anabaena* sep., *Peridinium* sp., other dinoflagellate species,

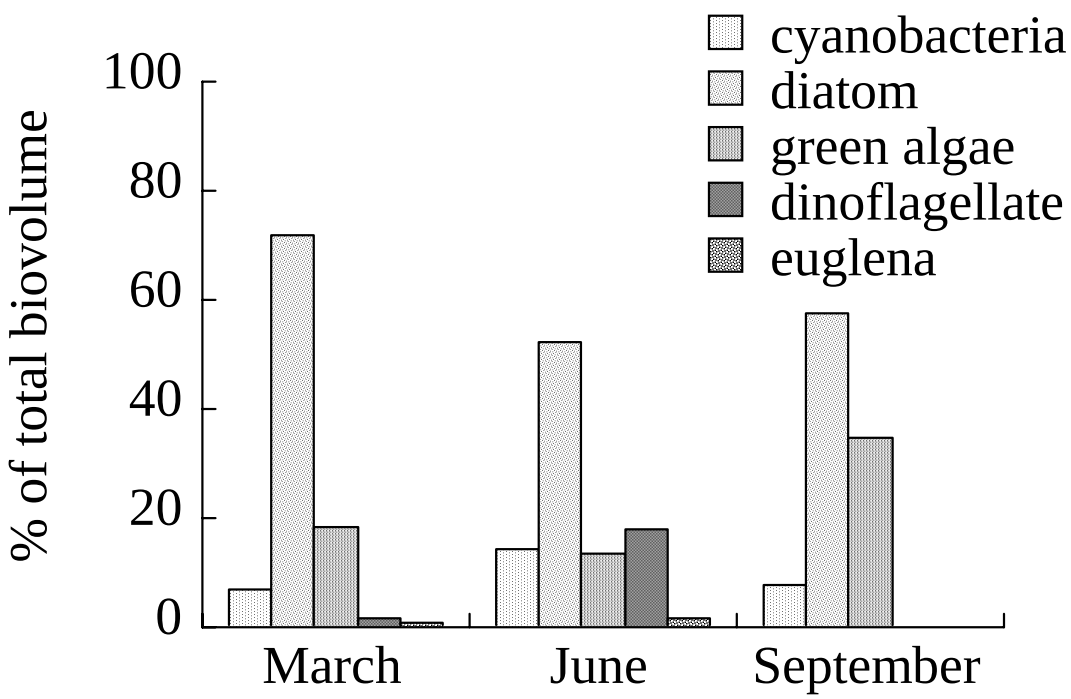

Fig. 8. Initial phytoplankton community composition placed into generic taxonomic groups of diatoms, cyanobacteria, green algae, dinoflagellates and *Euglena* in March, June and September. Graph shows only the abundant groups in each month.

Euglena sp., *Coscinodiscus* sp., *Skeletonema* sp., and *Odontella* sp. were present only in March and June. *Cryptomonad* sp., *Chlamydomonas* sp. and small centric diatoms were present only in September.

As with the zooplankton, similar responses to the treatments were observed in the phytoplankton, despite differences in community structures between experiments. The 1-day pulsed treatments showed higher maximum and integrated total phytoplankton biovolume (~2 fold) in all experiments compared to 3-day pulsed treatments (Fig. 9).

But at the 5% level, this trend was not significant in the June experiment (Table 4).

Closer examination of each experiment showed that diatoms, *Nitzschia closterium* and *Entomoneis* sp., and coccoid forms of green algae dominated the phytoplankton in March, and both showed significantly greater accumulation of biomass in the 1-day pulsed treatments. Diatoms, *N. closterium* and *Entomoneis* sp., and dinoflagellates, *Peridinium* sp., dominated in June, but only dinoflagellates showed significantly greater accumulation of biomass in the 1-day pulsed treatments. And finally, diatoms, *Entomoneis* sp. and *Chaetoceros* sp., dominated the third experiment. In March and June there were not significant size differences between diatom species. In September small sized phytoplankton dominated the assemblage.

In all experiments, 1-day pulses resulted in decreased species diversity relative to 3-day pulses (Fig. 10). Abrupt dips in diversity during the March and June experiments coincided with population shifts.

Discussion

With one notable exception (discussed in the next paragraph), trends observed across my experiments supported the model simulations of Roelke (2000), which predicted enhanced zooplankton populations, lower phytoplankton biovolume, and higher phytoplankton species diversity under conditions of pulsed inflow with a 3-day period compared to inflows delivered daily. My experimental results, however, are contradictory to previous observations from in-situ experiments (Flöder and Sommer 1999), where zooplankton populations showed no response to pulsed nutrient additions.

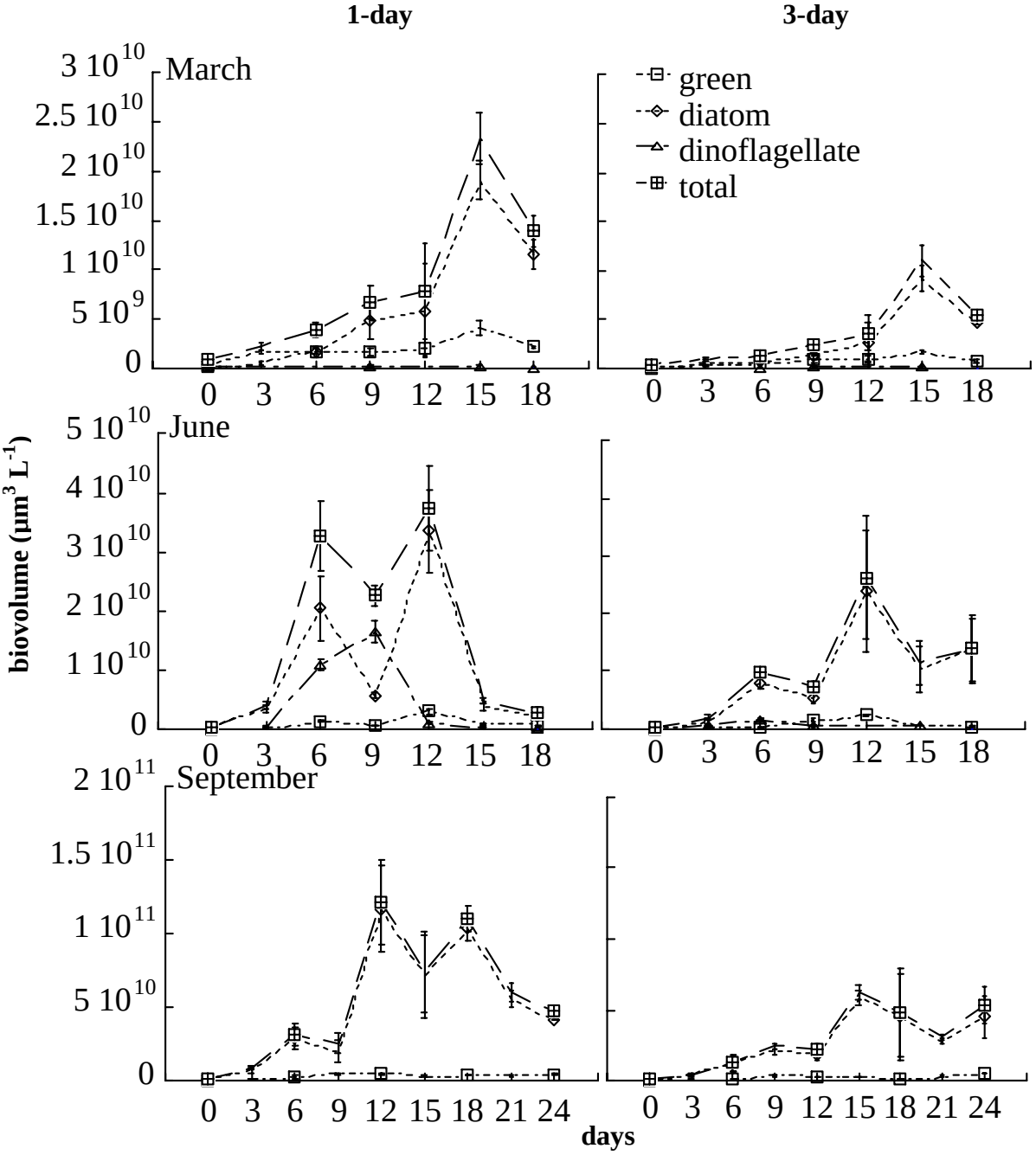

Fig. 9. Accumulation of phytoplankton biovolume in semi-continuous design experiments conducted in March, June and September. Symbols and error bars indicate the mean ± 1 SD for 1-day and 3-day pulse inflow treatments on triplicate chambers.

Table 4. Phytoplankton biovolume accumulation in 1-day vs. 3-day pulsed flow treatments for March, June and September experiments. The table lists the experiment, phytoplankton groups and results of one-way ANOVA that used variables of maximum phytoplankton population (a) and integrated phytoplankton population over the entire period of experiment (b) (the mean difference is significant at the .05 level; * = not significant; *I* = groups not abundant).

Experiment	**Phytoplankton groups**	***F(a)*** (max.)	***p(a)*** (max.)	***F(b)*** (integ.)	***p(b)*** (integ.)
March 2001	*Cyanobacteria*	105.01	.000	818.49	.000
	Green algae	127.78	.000	1338.65	.000
	Diatoms	56.85	.001	58.30	.001
	Dinoflagellates	3.00	.153	19.67	.011
	Total	113.30	.000	91.23	.000
June 2001	*Cyanobacteria*	1.36	.307*	34.37	.004
	Green algae	4.76	.094*	4.92	.091*
	Diatoms	1.76	.254*	0.26	.637*
	Dinoflagellates	203.96	.000	342.55	.000
	Total	3.07	.154*	6.48	.063*
Sept 2001	*Cyanobacteria*	2.24	.208*	2.05	.224*
	Green algae	0.22	.657*	11.86	.026
	Diatoms	22.73	.009	38.02	.004
	Total	26.24	.007	44.28	.003

In these experiments, however, *Daphnia* were prevalent. Large bodied zooplankton, such as *Daphnia*, are known to buffer plankton communities against nutrient perturbations (Cottingham and Schindler 2000). Large bodied zooplankton were present in my experiments, in the form of adult copepods, but they did not appear to exert the same top-down control as previously observed for *Daphnia*, and this might have allowed the plankton community to respond to the pulsed inflows.

The notable exception, where my experimental findings did not follow all of the model predictions, occurred in the June experiment. While zooplankton populations

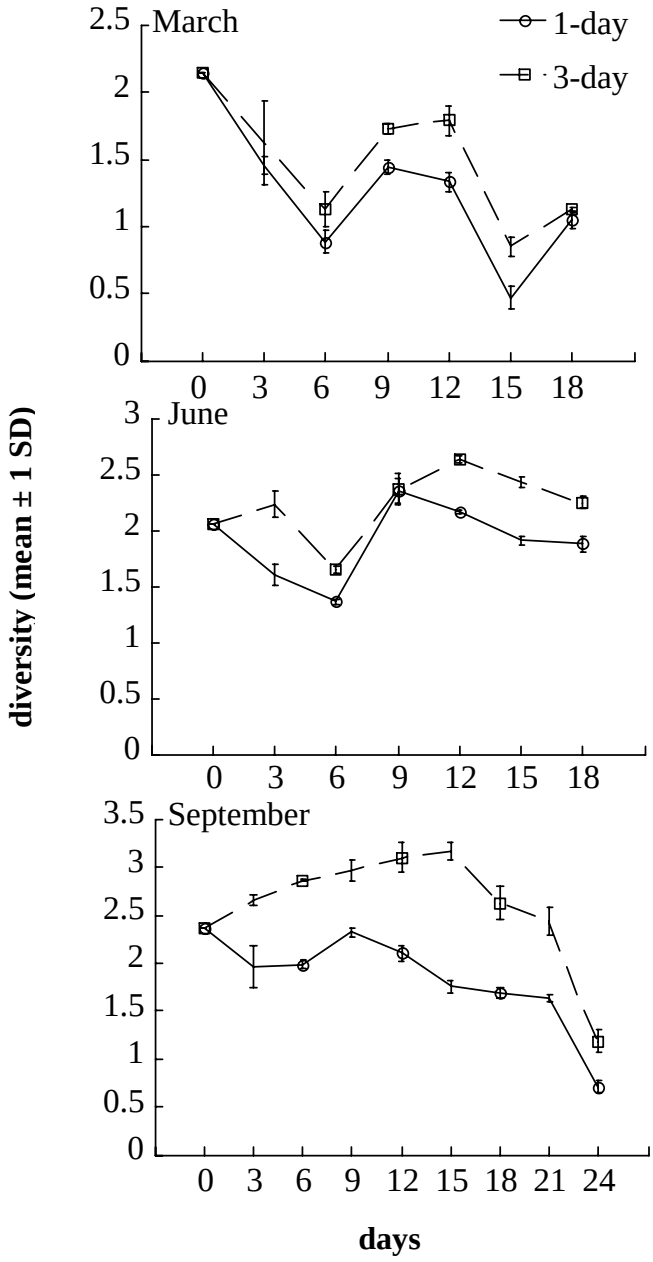

Fig. 10. Phytoplankton species diversity in semi-continuous design experiments conducted in March, June and September. 1-day pulse flow resulted in low diversity when compared to 3-day pulse flow. Symbols and error bars indicate the mean ± 1 SD for 1-day and 3-day pulse inflow treatments on triplicate chambers.

were enhanced and phytoplankton species diversity was elevated in the treatments receiving 3-day pulsed inflows, there was no reduced total phytoplankton biovolume. Note that dinoflagellate biovolume was reduced, but diatom biovolume was not. It is unclear why this occurred. For example, the diatoms in the March experiment were readily grazed, and the same two genera, *N. closterium* and *Entomoneis* sp. dominated the diatom communities in March and June. Furthermore, diatom cell sizes were indistinguishable between the two experiments. It might have been that zooplankton were grazing on diatoms in both treatments of the June experiment, but that diatom growth rates were in excess of zooplankton grazing. Consequently, no significant difference in diatom biovolume between treatments was observed. Increased zooplankton populations in the 3-day pulsed treatments were likely supported by grazing on dinoflagellates, as well as grazing on protozoa (Sterner and Hessen 1989; Ingrid et al. 1996).

Rotifer populations were much more prevalent in the September experiment. Heavy rains preceded my field sampling in September. Previous studies have shown that increased performance of rapidly-growing and edible phytoplankton forms, which are often of smaller cell size, typically follow favorable nutrient perturbations (Reynolds 1984; Sommer et al. 1986; Roelke et al. 1997). Phytoplankton of small cell size were much more prevalent in the September experiment, and this likely favored rotifers, which reproduce more rapidly than copepods and prefer prey of smaller cell size (Reynolds 1984; Sterner 1989; Horne and Goldman 1994). Despite major differences in phytoplankton and zooplankton community structure between the September experiment

and the March and June experiments, predictions of the model (Roelke 2000) were still observed, i.e., zooplankton populations were higher, phytoplankton biovolume was lower, and phytoplankton species diversity was higher under conditions of 3-day pulsed inflows.

My experimental design did not allow for determination of the mechanisms underlying my observations. Nevertheless, I offer a brief discussion regarding likely factors. Greater zooplankton populations in the 3-day pulsed inflow treatments likely resulted because prey diversity was greater, and prey-quality might have been higher. Copepods and rotifers are selective feeders (Reynolds 1984; Sterner 1989), and would have benefited by having a more diverse prey assemblage to select from. Food-quality in the 3-day pulsed treatments might have been higher as well, for two reasons. First, nutrient uptake and storage by phytoplankton was likely higher under the greater fluctuating physicochemical conditions that occurred in the 3-day pulsed treatments (Ketchum 1939; Droop 1968; Droop 1983). And second, higher grazing activity would have resulted in greater consumer-driven nutrient re-cycling, which would have prevented depletion of phytoplankton intracellular nutrient stores (Elser et al. 1998; Carpenter et al. 1993; Elser and Urabe 1999). Diminished phytoplankton biovolume in the March and September experiments likely resulted from greater grazing pressure, and elevated phytoplankton diversity likely resulted from suppression of competitive exclusion processes by fluctuating physicochemical conditions and top-down control (Hutchinson 1961; Tilman 1977; Reynolds 1984; Sommer 1989).

In conclusion, my experimental findings and the model simulations of Roelke

(2000) indicate that, in theory, pulsed inflows might alter plankton dynamics by stimulating energy transfer up the food web, i.e., through greater zooplankton productivity, and prevent excessive accumulation of phytoplankton (algal blooms), i.e., through reduced phytoplankton biovolume and elevated diversity. In-field mesocosm experiments, where the complexity of the natural environment can better be replicated, are needed to verify these theoretical findings. It may be that benthic algae and zoobenthic communities respond in a similar manner, as suggested previously (Hann and Goldsborough 1997). Findings of this nature would have profound implications to management of coastal wetland and bay systems in watersheds where freshwater inflows are compromised.

CHAPTER IV

INFLUENCE OF PULSED INFLOWS AND NUTRIENT LOADING ON NATURAL ZOOPLANKTON AND PHYTOPLANKTON ASSEMBLAGES: COMPARISON OF EXPERIMENTS USING SEMI-CONTINUOUS AND FLOW-THROUGH DESIGNS

Introduction

Environmental disturbances in aquatic systems, such as nutrient additions associated with inflow events, are known to influence phytoplankton community composition, species diversity, and biomass (Sommer 1986; Gaedeke and Sommer 1986; Flöder and Sommer 1999; Hambright and Zohary 2000). As a result changes in phytoplankton community structure can influence zooplankton community structure (Sommer et al. 1986; Steiner 2001; Buyukates and Roelke 2002). After an inflow event to a system where phytoplankton are nutrient-limited, succession from less edible, slower growing, k-selected species to more edible, faster growing, r-selected species might occur (Sommer 1981; Reynolds 1984; Sommer et al. 1986; Roelke et al. 1997), which may stimulate secondary productivity. Zooplankton community structure might shift because taxa of small body-size and short generation times, e.g., rotifers and protozoa, will likely be the first to respond to a shift in prey availability, and also the first to recover from flushing losses (Sommer et al. 1986; Reynolds 1984; Havens 1991a; Havens 1991b; Kim et al. 2002). In addition, high phytoplankton species diversity, which can be maintained in systems where the physicochemical environment

fluctuates, may result in the proliferation of preferential grazers (Reynolds 1984; Reynolds 1989), and again result in a shift in zooplankton community structure.

Zooplankton, however, might mask the effects of nutrient loadings on phytoplankton community structure. For example, strong top-down control exerted by non-selective grazers might prevent additional accumulation of phytoplankton biomass and prevent shifts in community composition (Reynolds 1984; Sterner 1989; Cottingham and Schindler 2000). In addition, through consumer-driven nutrient recycling, strong top-down control might remove nutrient limitation altogether, thereby negating the influence of nutrient additions to the system (Lehman 1988; Sterner 1989; Katechakis et al. 2002). Similarly, a well-established population of preferential grazers may control some phytoplankton populations that would have otherwise proliferated following a disturbance (MacKay and Elser 1998; Sounders et al. 2000; Kagami et al. 2002).

Many of these concepts were captured in a food web model of the Nueces River Estuary, TX (Roelke 2000). In the previous chapter, results from experiments of semi-continuous design using natural plankton assemblages from the Nueces Delta supported these theoretical findings. In these experiments, copepod adults and nauplii were the dominant grazers. Synchronous with these experiments, and using the same natural plankton assemblages, I conducted experiments using incubators with a flow-through design. In these experiments turbulence was greater, which resulted in substantial increased prevalence of rotifers and protozoa, and greatly diminished populations of copepods. Copepods and rotifers, while both selective grazers, differ in their preferred prey size ranges. Would the model predictions by Roelke (2000) hold up in the absence

of larger selective grazers, i.e., in an assemblage where r-selected phytoplankton forms of larger cell size would be able to grow unchecked? Here I compare succession patterns of plankton between the two types of experiments, and evaluate how the differing zooplankton community structure effected the influence of continuous vs. pulsed inflows on phytoplankton species diversity, zooplankton abundance, and phytoplankton biovolume.

Materials and methods

Three flow-through incubation experiments were conducted on 15 March, 7 June and 8 September, 2001 to test the influence of varying inflow and nutrient loading frequency and magnitude on zooplankton abundance, phytoplankton biovolume and species diversity. The inoculum that was used in the experiments consisted of a natural, mixed plankton assemblage from the Rincon Delta 27˚ 57' N, 97˚ 31' W (station 2). A detailed description of sampling, media preparation for the experiments and experiment set up was given in Chapter III.

Each of the three flow-through experiments was comprised of two treatments, continuous flow and pulsed flow (3-d period). Each treatment performed in triplicate. The flow-through chambers (Fig. 11) used in these experiments allowed for control of flushing rate and periodicity, nutrient loading magnitude and ratio, temperature, irradiance and photoperiod, and turbulence (Lampert 1976; Boraas 1980). Values for flushing rate and periodicity, as well as nutrient loading magnitude and ratio (for nitrogen and phosphorus only) were determined as mentioned in Chapters II and III.

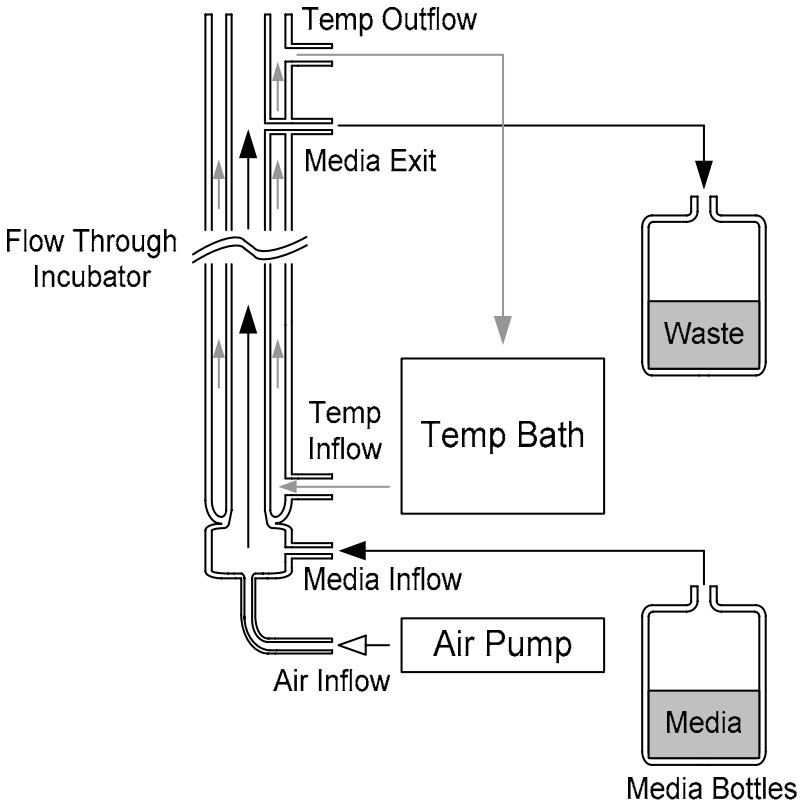

Fig. 11. Schematic diagram of the flow-through chamber design (redrawn from Buyukates and Roelke 2000). The design allows for control of flushing rate and periodicity, nutrient loading magnitude and ratio, temperature, irradiance and photoperiod and turbulence.

Flow rate and nutrient loading were controlled using peristaltic pumps. The volume of flow-through chambers was 365 ml. A constant hydraulic residence time of 0.11 d-1 was employed for the continuous flow chambers, while a periodic hydraulic residence time of 0.33 d^{-1} was employed for the pulsed flow chambers once every third day. In this way, the magnitude of flushing and nutrient loading over the course of the experiments was the same for the continuous and pulsed flow treatments. Only the mode of flushing and nutrient loading was different.

In the experiments, temperature, photoperiod and irradiance values were identical as semi-continuous design experiments. Turbulence was controlled using an aerator powered through a time delay relay (5 seconds on / 40 seconds off). This resulted in intermittent periods without disturbance, which provided adequate mixing to maintain a homogeneous environment for sampling. Part of the chambers, that periphyton growth and accumulation was likely to occur were covered with aluminum foil to prevent light penetration.

Samples for microscopic analyses were taken at 3-day intervals and preserved in 5 % glutaraldehyde, v/v. Plankton identification and counts were conducted using an inverted light microscope by the Utermöhl method (1958). Greater detail on microscopic analysis was provided in Chapter III. Shannon-Weaver index was used to estimate species diversity (Shannon and Weaver 1949). The biovolume for each of the size classes (<20, 20-100, 100-200, >200 μm) were estimated by summation of the population biovolume of algal species whose maximal linear dimensions fell within the classes (Havens 1991a).

Differences between continuous flow and pulsed flow chambers were quantified using one-way ANOVA tests (SPSS Inc. 1994). Two sets of ANOVAs were performed. In the first set, the dependent variables were the maximum zooplankton population and maximum phytoplankton biovolume that occurred in a chamber. In the second set, dependent variables were the zooplankton population and phytoplankton biovolume that were integrated over the entire period of experiment. The second set of ANOVAs accounted for the total performance of zooplankton and phytoplankton populations over

the course of the experiments. Significant differences were determined based on $p<0.05$.

Results

In the experiments, periphyton did not accumulate in any of the chambers. Therefore, shading or nutrient uptake by periphyton did not affect the following results.

Zooplankton abundance and structure in continuous vs. pulsed treatments

Despite differences in zooplankton community structure for each of the experiments, rotifers numerically dominated the macro-zooplankton in all experiments (Figs. 12, 13, 14). In all experiments similar responses to the treatments were observed. The maximum and integrated adult copepod and rotifer densities were significantly greater in pulsed flow treatments in all experiments (Table 5). The maximum and integrated nauplii and protozoa did show significantly greater densities in the March and June experiments but did not differ among treatments in the September experiment (Table 5).

Mean size distribution for adult copepods, nauplii, rotifer and protozoa did not show significant differences among treatments. Therefore it is reasonable to approximate population density as zooplankton population biomass in these experiments.

Phytoplankton biovolume and composition in continuous vs. pulsed treatments

Phytoplankton community composition varied between experiments. A detailed description of community structure was given in the previous chapters. Despite differences in community structure similar responses were observed in the phytoplankton as with the zooplankton. The continuous flow treatments showed higher

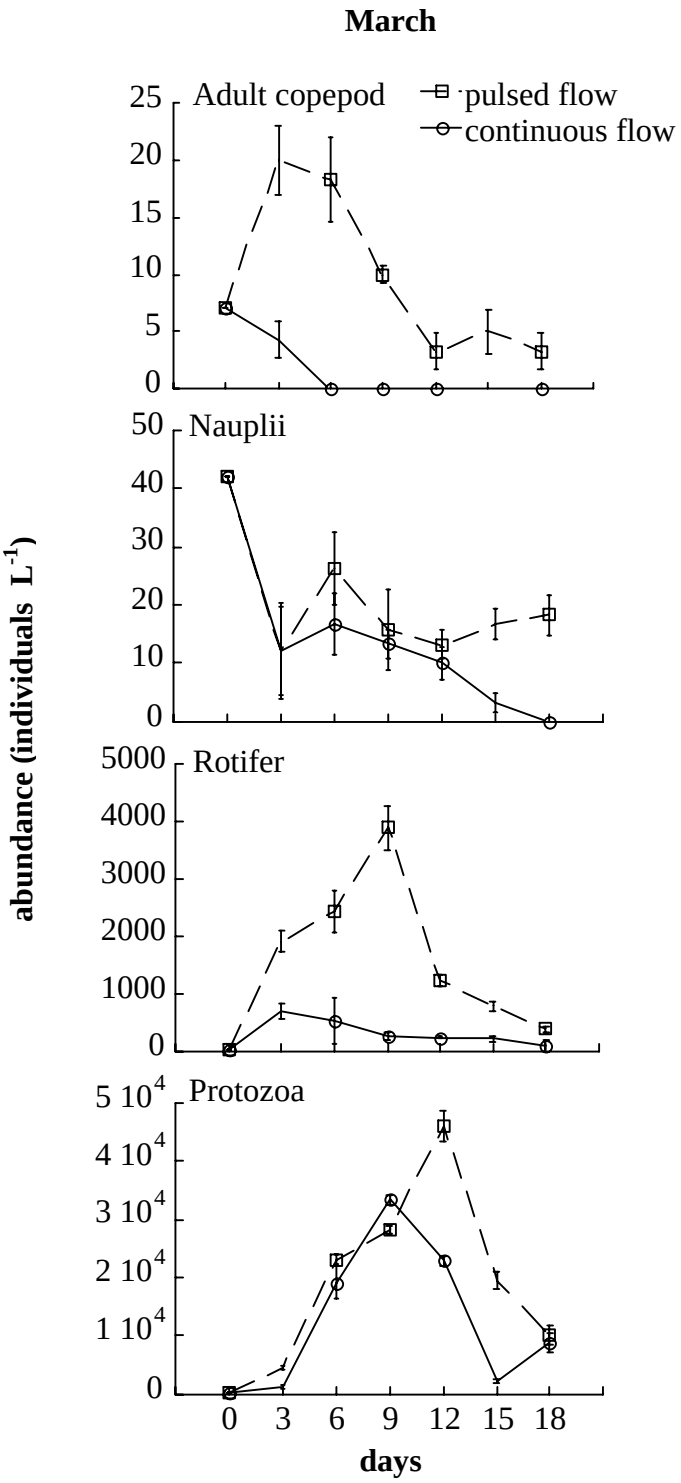

Fig. 12. Changes in adult copepod, nauplii, rotifer and protozoa abundance in continuous flow and pulsed flow treatments in March. Symbols and error bars indicate the mean ± 1 SD for continuous flow and pulsed flow treatments on triplicate chambers.

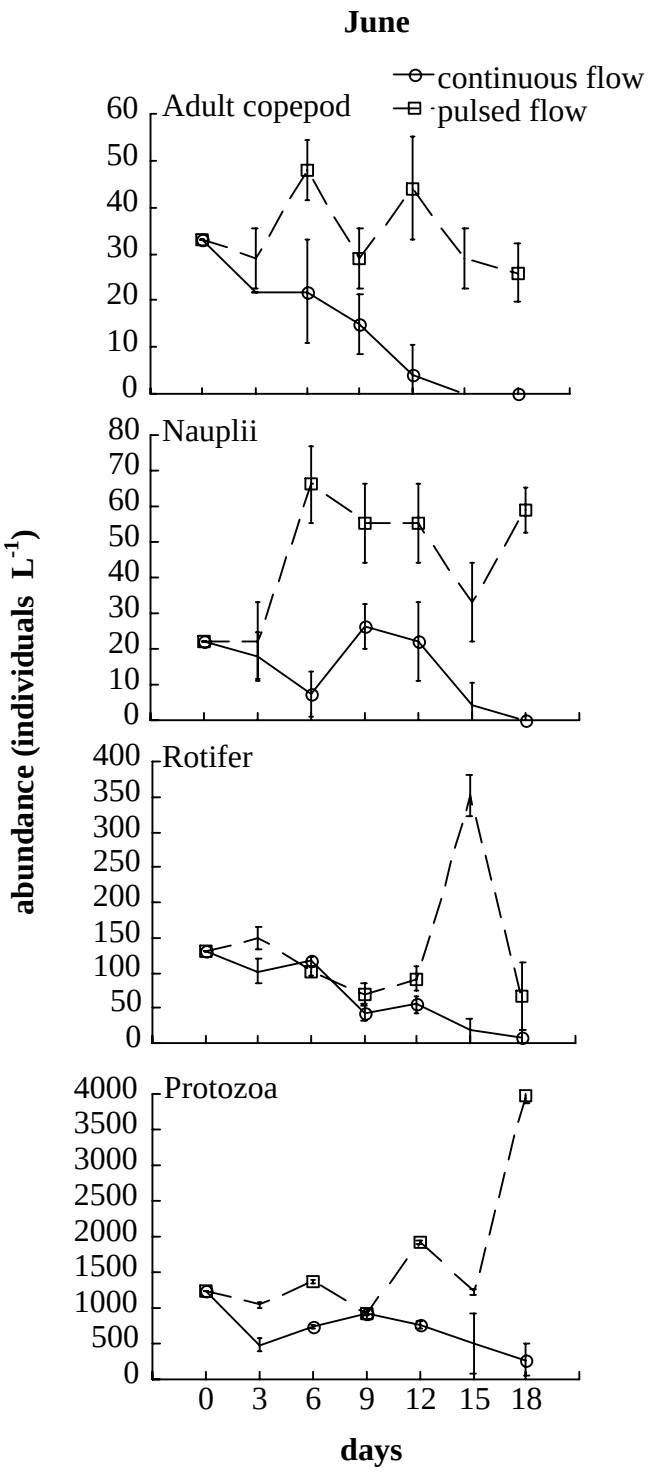

Fig. 13. Changes in adult copepod, nauplii, rotifer and protozoa abundance in continuous flow and pulsed flow treatments in June. Symbols and error bars indicate the mean ± 1 SD for continuous flow and pulsed flow treatments on triplicate chambers.

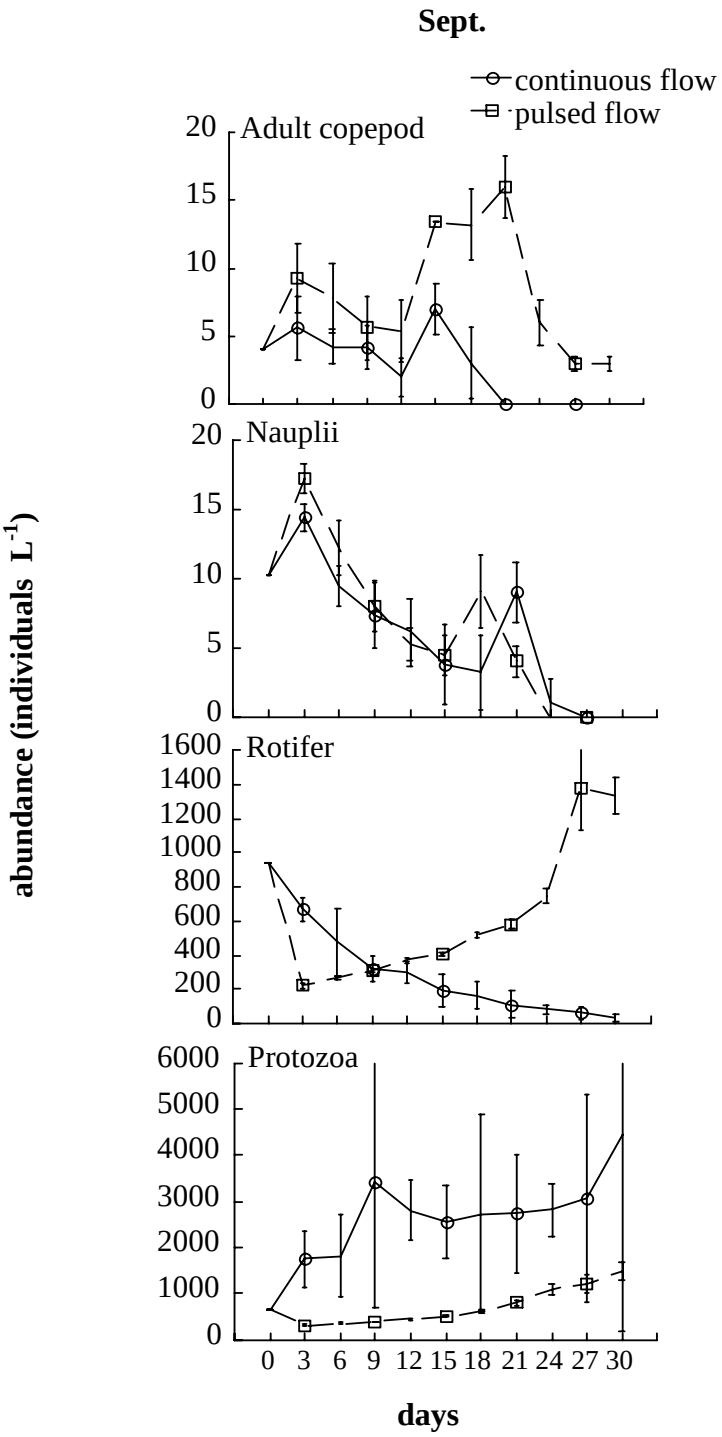

Fig. 14. Changes in adult copepod, nauplii, rotifer and protozoa abundance in continuous flow and pulsed flow treatments in September. Symbols and error bars indicate the mean ± 1 SD for continuous flow and pulsed flow treatments on triplicate chambers.

Table 5. Zooplankton population responses in continuous vs. pulsed flow treatments for March, June, September experiments. The table lists the experiment, zooplankton groups and results of one-way ANOVA that used variables of maximum zooplankton population (a) and integrated zooplankton population over the entire period of experiment (b) (the mean difference is significant at the .05 level; * = not significant).

Experiment	**Zooplankton groups**	***F(a)*** (max.)	***p(a)*** (max.m)	***F(b)*** (integ.)	***p(b)*** (integ.)
March 2001	Adult copepod	32.00	.0048	48.68	.0027
	Nauplii	16.45	.0154	294.36	.0001
	Rotifer	134.90	.0003	226.02	.0001
	Protozoa	48.90	.0022	73.19	.0010
June 2001	Adult copepod	24.50	.0078	108.64	.0005
	Nauplii	25.00	.0075	68.31	.0012
	Rotifer	186.18	.0002	239.04	.0001
	Protozoa	1397.24	.0000	313.91	.0001
Sept 2001	Adult copepod	89.29	.0007	134.83	.0003
	Nauplii	0.20	.6751*	0.02	.8827*
	Rotifer	88.54	.0007	79.56	.0009
	Protozoa	5.08	.0871*	5.01	.0897*

maximum and integrated total phytoplankton biovolume (~ 2 fold) in all experiments compared to pulsed treatments (Fig. 15). But at the 5 % level, this trend was not significant in the September experiment (Table 6).

More detailed analysis of the phytoplankton community structure in each experiment showed that coccoid and oblong forms of green algae and diatoms, *Pleurosigma* sp., *Gyrosigma* sp. and *Navicula* sp. dominated the phytoplankton in March, and both showed significantly greater accumulation of biomass in the continuous flow treatment. Dinoflagellates did not show significant differences and chrysophytes did only occur at the last sampling time in pulsed flow treatments. *Gloeocystis* sp.,

coccoid and oblong forms of green algae, diatoms, *Nitzschia* sp. and *Skeletonema* sp., an unidentified dinoflagellate species dominated in June. Dinoflagellates and maximum diatom biomass showed significantly greater accumulation in continuous flow treatments. Finally, various species of green algae and centric forms of diatoms, *Nitzschia* sp., and *Navicula* sp. dominated in September, but only diatoms showed significantly greater accumulation of biomass in the continuous flow treatments. Phytoplankton species diversity showed similar trends in the March and June experiments (Fig. 16). During the March experiment, continuous flow resulted in a continued decrease in phytoplankton species diversity, while the chambers receiving pulsed flows showed a dramatic decrease after the first pulse, then an increase in phytoplankton species diversity (Fig. 16). This dramatic decrease in diversity at the first pulsed flow event coincided with a rapid increase in *Navicula* sp. and coccoid forms of green algae. Continued decrease of phytoplankton species diversity observed in the continuous flow chambers was due to the gradual accumulation of large diatoms, especially *Pleurosigma* sp. and *Gyrosigma* sp. In the June experiment, continuous flow resulted in decreased phytoplankton species diversity while higher diversity was observed in the pulsed flow chambers (Fig. 16). An abrupt decrease in diversity in the fourth sampling time of pulsed flow coincided with the accumulation of *Nitzschia* species, especially *Nitzschia closterium* and *Nitzschia longissima*. Low diversity in the continuous flow chambers was due to the abundance of an unidentified dinoflagellate species. In the September experiment as the diatom and green algal bloom ensued phytoplankton species diversity decreased in both treatments (Fig. 16).

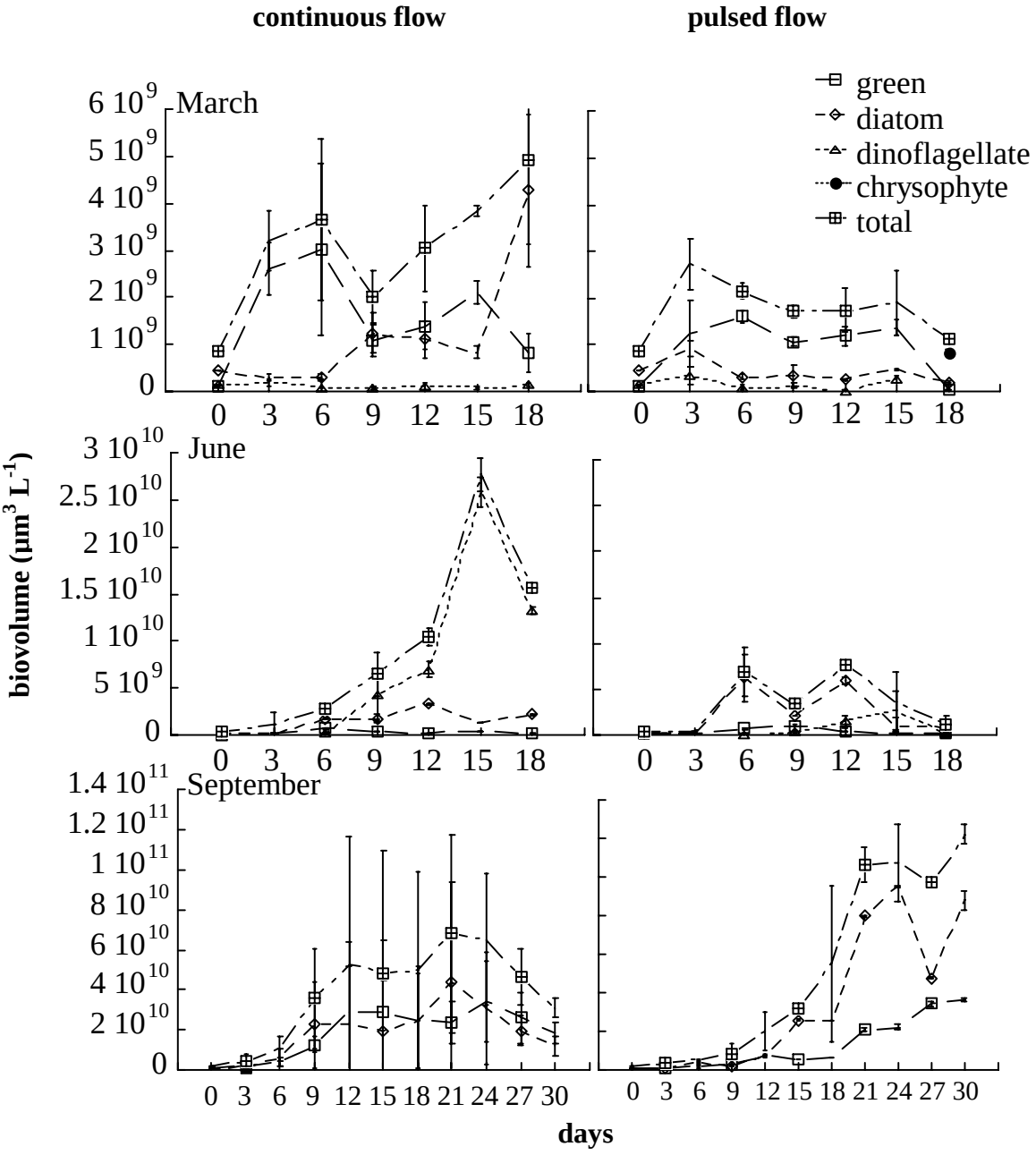

Fig. 15. Accumulation of phytoplankton biovolume in flow-through incubation design experiments conducted in March, June and September. Symbols and error bars indicate the mean ± 1 SD for continuous flow and pulsed flow treatments on triplicate chambers.

Table 6. Phytoplankton biovolume accumulation in continuous vs. pulsed flow treatments for March, June and September experiments. The table lists the experiment, dominant phytoplankton groups and results of one-way ANOVA that used variables of maximum phytoplankton population (a) and integrated phytoplankton population over the entire period of experiment (b) (the mean difference is significant at the .05 level; * = not significant).

Experiment	**Phytoplankton groups**	***F(a)*** (max.)	***p(a)*** (max.)	***F(b)*** (integ.)	***p(b)*** (integ.)
March 2001	Green algae	12.70	.024	13.88	.020
	Diatoms	12.54	.024	15.53	.017
	Dinoflagellates	2.29	.205*	4.30	.107*
	Total	8..37	.044	12.37	.025
June 2001	Green algae	7.52	.051*	3.63	.123*
	Diatoms	13.87	.020	6.15	.068*
	Dinoflagellates	379.61	.000	189.35	.000
	Total	241.95	.000	79.61	.000
Sept2001	Green algae	0.04	.852*	0.65	.466*
	Diatoms	12.48	.024	15.02	.018
	Total	1.03	.368*	0.76	.432*

Accumulation of phytoplankton biovolume in the September experiment varied from the first two experiments (Fig. 15). In both treatments of the third experiment diatoms and green algae dominated the phytoplankton, and accumulated in biovolume to a level that was an order of magnitude greater than the previous two experiments. Except for the continuous flow treatment in the September experiment, variability within treatments was low. In this experiment, however, the magnitude and the timing of the maximum biovolume, and the phytoplankton composition at the genus level differed among chambers within the continuous flow treatment. In the first chamber *Nitzschia*

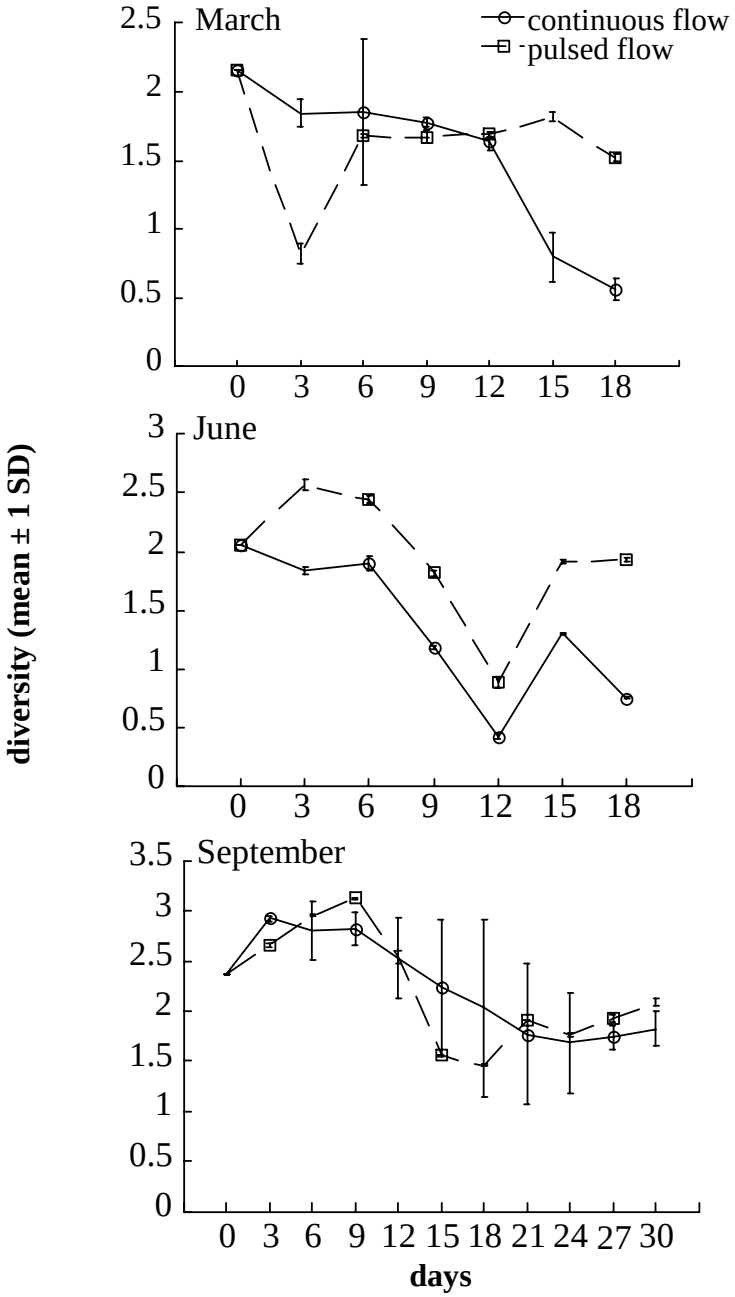

Fig. 16. Phytoplankton species diversity in experiments conducted in March, June and September. Continuous flow resulted in low diversity when compared to pulsed flow. Symbols and error bars indicate the mean ± 1 SD for continuous flow and pulsed flow treatments on triplicate chambers.

sp., *Navicula* sp., *Characium* sp. and *Ankistrodesmus* sp. were the prevalent genera. In the second chamber phytoplankton structure was comprised of a combination of centric diatoms, *Nitzschia* sp., *Navicula* sp., *Characium* sp., *Entomoneis* sp., *Tetraedron* sp., *Gloeocystis* sp. and *Franceia droescheri*. In the third chamber *Nitzschia* sp., *Entomoneis* sp. and *Franceia droescheri* were the prevalent genera.

Comparison of semi-continuous and flow-through design experiments

Overall response, in terms of zooplankton abundance, phytoplankton biovolume and phytoplankton species diversity, was consistent between the semi-continuous experimental design and the flow-through incubation design. Phytoplankton and zooplankton community composition, however, varied between the experimental designs, despite the near-identical initial conditions. For example, diatoms dominated in all treatments using the semi-continuous experimental design, whereas green algae, dinoflagellates and diatoms dominated in the March, June and September experiments of flow-through design, respectively (Figs. 17, 18, 19).

In the March and June experiments, adult copepods and nauplii were numerically dominant in the semi-continuous design, and rotifers dominated the September experiment. In the flow-through design experiments, rotifers numerically dominated all experiments (Figs. 12, 13, 14). Finally, protozoa did not do well in experiments of semi-continuous design relative to the experiments of flow-through design (Figs. 17, 18, 19).

Grazing pressure induced shifts in phytoplankton cell-size was observed in both types of designs (Figs. 17, 18, 19). However, the shift from smaller to larger cell-size was more prevalent in the semi-continuous experiments, in which the adult copepods

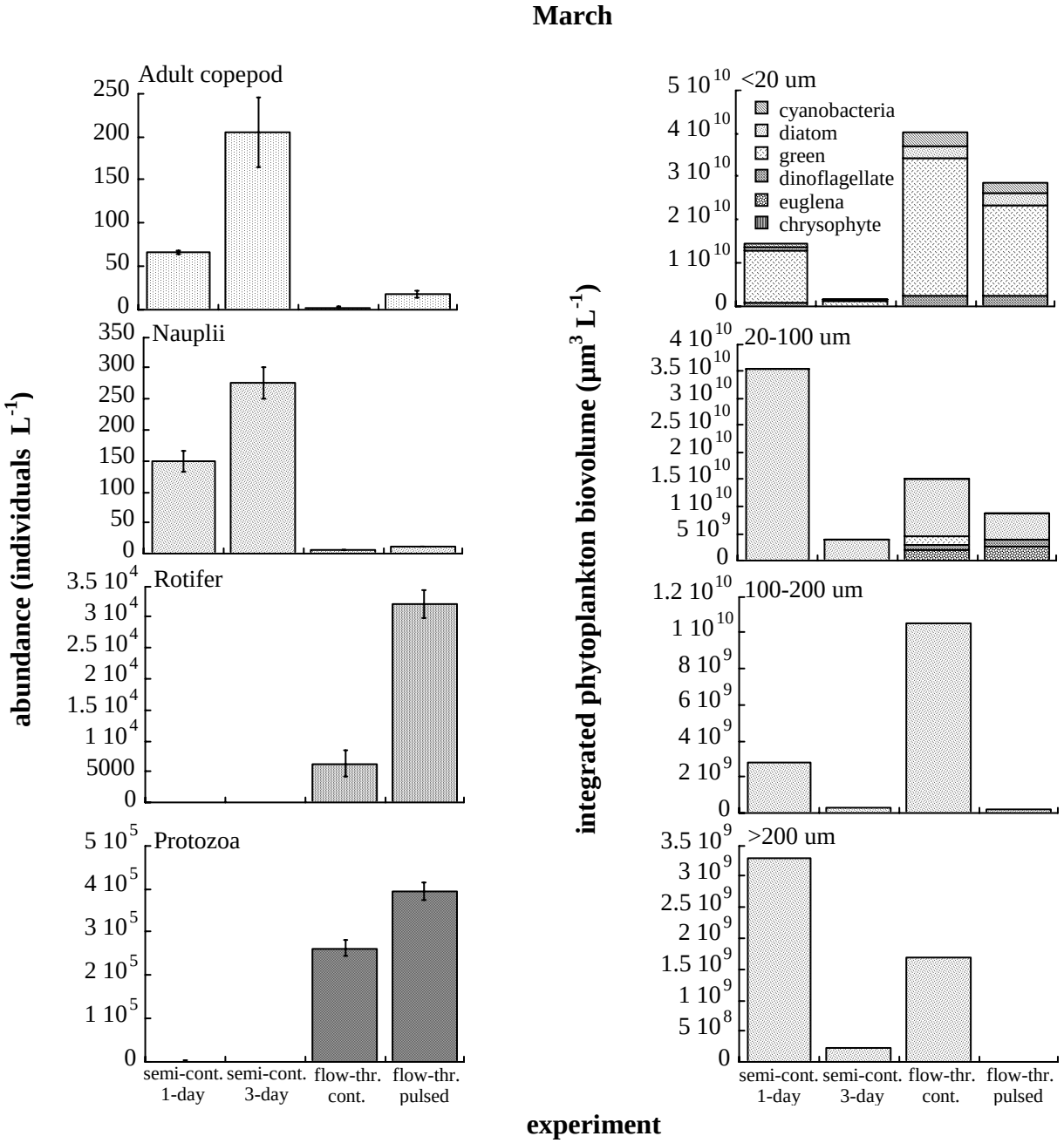

Fig. 17. Comparison of zooplankton group structure and phytoplankton cell size between semi-continuous design and flow-through design experiments conducted in March.

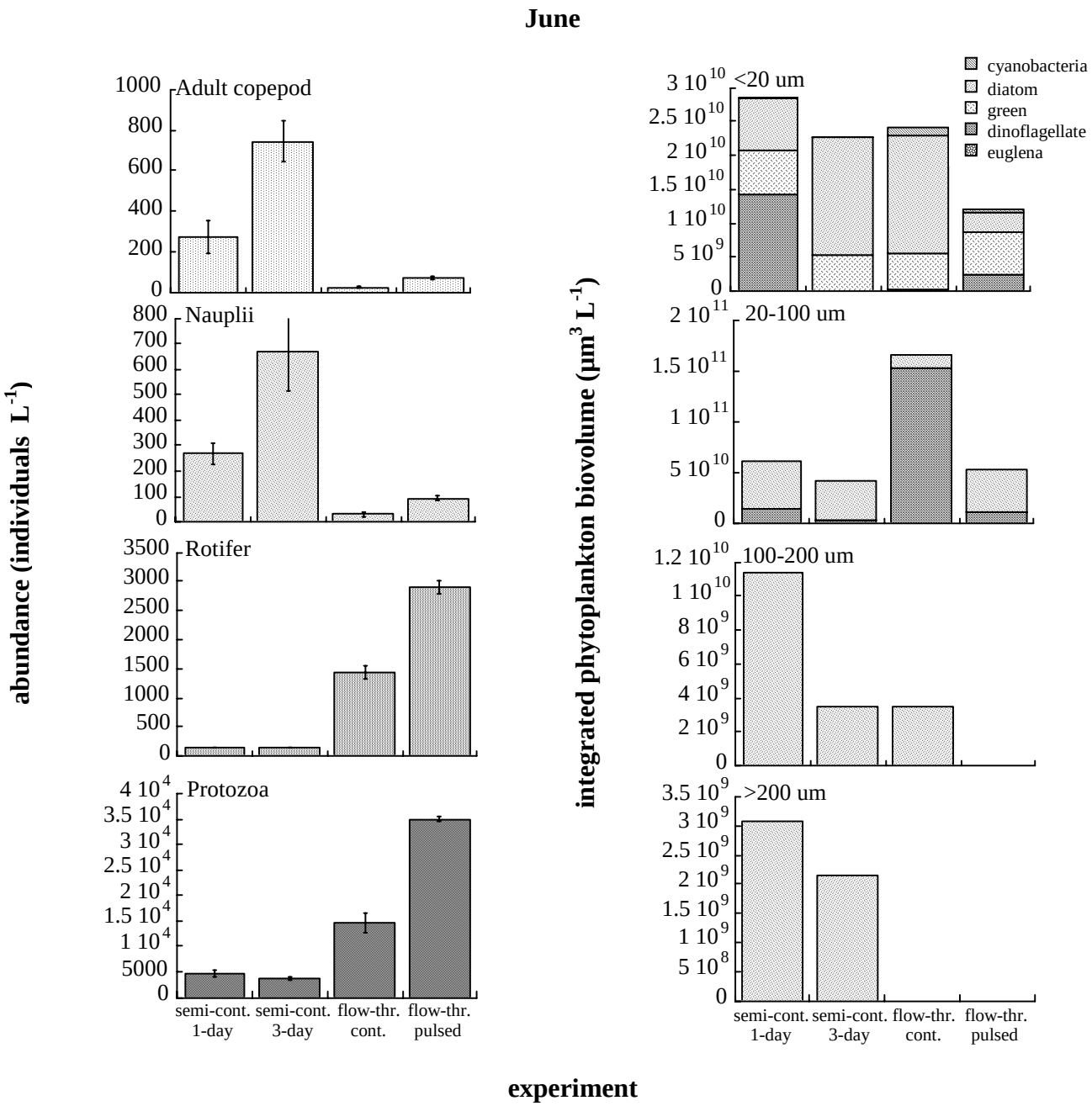

Fig. 18. Comparison of zooplankton group structure and phytoplankton cell size between semi-continuous design and flow-through design experiments conducted in June.

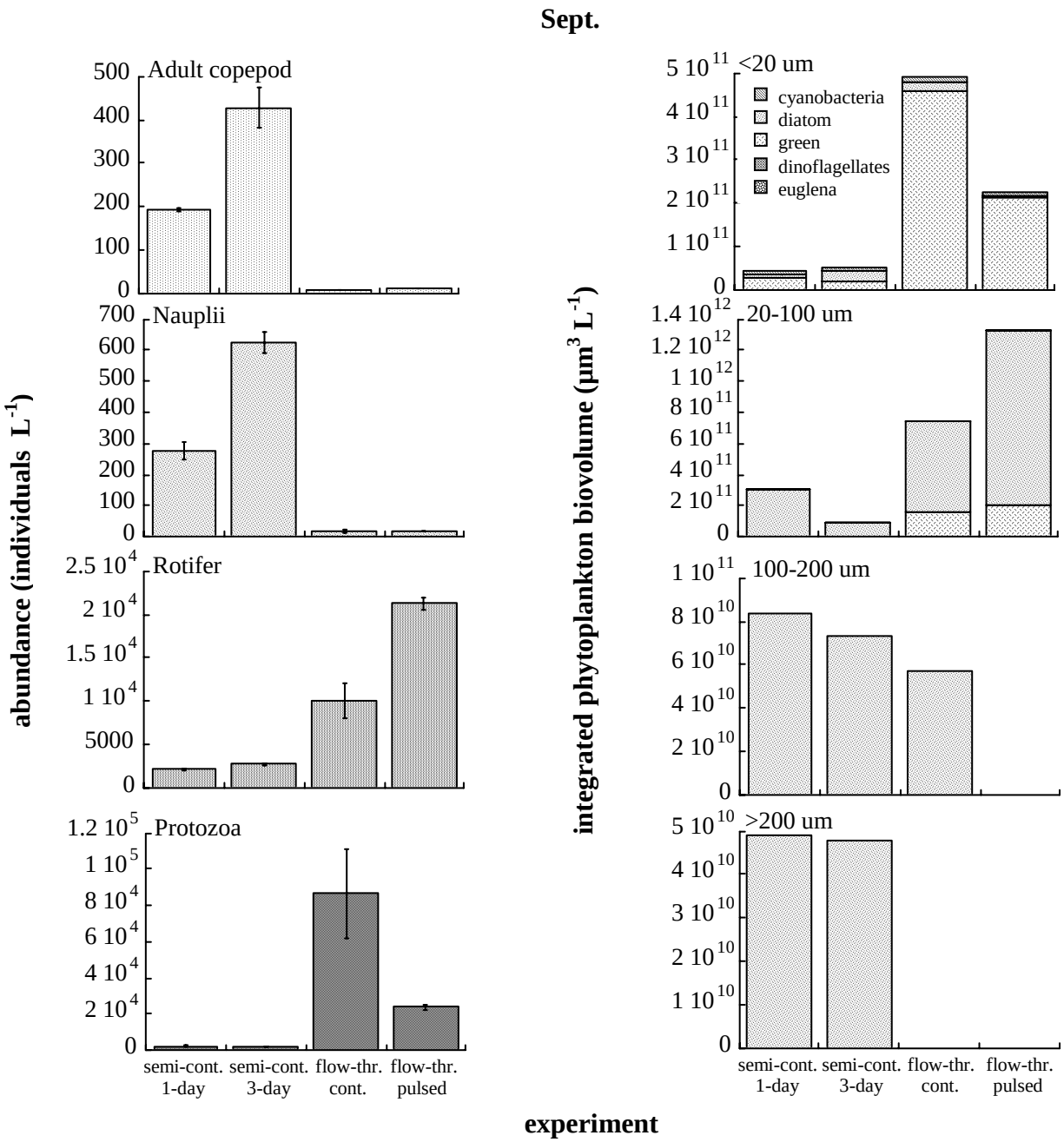

Fig. 19. Comparison of zooplankton group structure and phytoplankton cell size between semi-continuous design and flow-through design experiments conducted in September.

and nauplii were dominant, compared to flow-through experiments, where rotifers dominated.

Discussion

The experiments showed that despite differences in zooplankton structure and phytoplankton community composition between the two experiment designs, trends in the model predictions by Roelke (2000) were supported. That is, secondary productivity and phytoplankton species diversity was higher under pulsed inflow and nutrient loading conditions. It may be that in both experimental designs, phytoplankton was of higher quality in the 3-day pulsed treatments, and this resulted in enhanced zooplankton growth. Another alternative explanation is that the increased diversity in 3-day pulsed treatments might have offered selective grazers a better environment, i.e., a broad range of phytoplankton to choose from.

In the March and June experiments of semi-continuous design and flow-through design, adult copepods and nauplii dominated the former, while rotifers dominated the latter. This result was likely due to the lower turbulence in the experiments of semi-continuous design, which might have favored copepod feeding and growth (Saiz and Alcaraz 1991; Alcaraz 1997; Petersen et al. 1998; Quintana et al. 1998). In addition, copepod adults can graze on rotifers, and also protozoa (Sterner 1989; Ingrid et al. 1996). It is likely that grazing by adult copepods contributed to the lower abundance of rotifers and protozoa in the March and June semi-continuous experiments.

In the September experiment, both designs were dominated by rotifers. Water

was collected for this experiment shortly after a heavy rain event in the watershed. Salinity was low and nutrient concentrations were high. Various species of rotifers, and small, fast growing, r-selected phytoplankton dominated the plankton assemblage at this time. Previous studies showed that when food sources and physical conditions are favorable for rotifers, they could reproduce rapidly (Reynolds 1984; Gilbert 1985; Sterner 1989). In this way, rotifers can out-pace grazing pressure exerted by slower growing copepods, and come to numerically dominate the zooplankton community. Consequently, for the September semi-continuous design and flow-through design experiments, grazer pressure as a function of zooplankton community structure, were similar.

Because zooplankton structure varied between the March and June experiments of semi-continuous design and flow-through design, the phytoplankton assemblages were subjected to different selective grazing pressure. For example, copepod adults and nauplii can graze on the same size and structure range of phytoplankton that are susceptible to rotifer grazing, but copepods are able to graze on larger phytoplankton species as well (Reynolds 1984; Sterner 1989).

Effects of differing grazing pressure between the two experiment designs for the March and June experiments were reflected in the phytoplankton succession trajectories. Although strong grazing pressure caused an increase in phytoplankton cell size in both types of experimental designs, shifts from smaller to larger cell-size was more prevalent in the semi-continuous design, in which the adult copepods and nauplii were dominant, compared to flow-through design, where rotifers dominated. This trend was strongest in

the 3-day pulse treatments, where large diatoms were main survivors in the semi-continuous design (see Chapter III), and some combination of large diatoms, colonial green algae and dinoflagellates dominated the flow-through design. Even though zooplankton community structure was alike in both designs, the same phytoplankton cell-size shift observed in the March and June experiments was observed in the September experiment. Although rotifers dominated both semi-continuous and flow-through designs, the semi-continuous design had a more pronounced phytoplankton cell-size shift. Most likely, this was due to the presence of some copepods in the semi-continuous experiment, although not as much as the previous two semi-continuous experiments. These results are consistent with the hypothesis that phytoplankton community structure moves toward dominance of larger species under strong grazing pressure due to increased body size or biomass of zooplankton population (Carpenter and Kitchell 1984; Bergquist et al. 1985; Carpenter et al. 1993). Again consistent with the model predictions of Roelke (2000), accumulation of grazer populations and phytoplankton species diversity was higher in the 3-day pulse treatments in both types of experiment designs.

Higher phytoplankton species diversity in treatments receiving pulsed inflows might be a result of top-down control and fluctuating abiotic conditions. For example, selective feeding on the most abundant phytoplankton species would prevent exclusion of slower-growing species, thereby maintaining diversity (Sommer et al. 1986; Gismervik and Andersen 1997; Sommer and Stibor 2002). This process would exert greater influence on phytoplankton diversity with higher zooplankton populations.

Similarly, fluctuating physicochemical conditions, which would have occurred in the pulsed inflow treatments, are known to constrain competitive exclusion and promote coexistence (Hutchinson 1961; Sommer et al. 1986; Sommer et al.1993).

In summary, through comparison of experiments of semi-continuous and flow-through design, I showed that pulsed inflows supported greater accumulation of some grazer populations and higher phytoplankton species diversity, when zooplankton were dominated by rotifers or by copepods. The results of this study are consistent with previous model predictions (Roelke 2000). Further experiments are needed to determine whether this relationship holds true when non-selective grazers dominate the zooplankton community structure.

CHAPTER V

FUNDAMENTAL PREDICTABILITY IN MULTI-SPECIES COMPETITION: THE INFLUENCE OF RESOURCE STORAGE

Introduction

One of the main goals of ecology is to understand the mechanisms that impact biodiversity. Classical competitive exclusion theory (Hardin 1960) predicts that the number of coexisting species can not exceed the number of limiting resources at equilibrium. Because this equilibrium is never or rarely if ever obtained in natural habitats, the number of coexisting species often exceeds the number of limiting resources (Hutchinson 1961; Sommer 1984). Particularly in aquatic systems, Hutchinson (1961) suggested that environmental fluctuations or disturbances would suppress competitive exclusion processes in plankton communities, thereby maintaining higher species diversity.

Alternative to this traditional belief, Huisman and Weissing (1999, 2000, 2001a, 2001b) recently suggested that multiple species competing for multiple abiotic resources could generate competitive chaos or oscillations, which may allow the coexistence of many species. In their models Huisman and Weissing assumed that the specific growth rates of phytoplankton species are characterized according to the Monod equation (Monod 1950):

$$\mu = \mu_{max}\left(\frac{S}{S + k_s}\right) \tag{7}$$

where μ is the growth rate, μ_{max} is the nutrient saturated growth rate, k_s is the half saturation constant, and S is the dissolved nutrient concentration. It is practical to use the Monod equation since it relates the growth rate (μ) of a phytoplankton species to the dissolved nutrient concentration of the limiting nutrient (S), which is an easy parameter to measure (Sommer 1989; Sommer 1991). However, Droop (1973, 1983) proved that the Monod model is only applicable under steady state conditions, i.e., chemostat cultures. Therefore, the Monod model is not a good representative of the nature under fluctuating conditions, where luxury consumption and storage of nutrients may alter the growth of phytoplankton species (Droop 1973; Droop 1983; Sommer 1989; Sommer 1991). Thus, despite the difficulty of measuring individual cell quotas of species, in theory Droop's cell quota model is a better representation of the natural environment,

$$\mu = \mu_{max}\left(1 - \frac{Q_{min}}{Q}\right) \tag{8}$$

where Q_{min} is the minimal cell quota, Q is the cell quota, and other symbols are as previously described.

Here I rebuilt the model of Huisman and Weissing (2001b) and tested their predictions under the conditions of "three species competing for three resources" to study the effects of resource storage on competition of multiple phytoplankton species on multiple resources. I compared the Monod equation with Droop's cell quota equation and examined whether resource storage reduced the opportunity for chaotic fluctuations or added additional non-linearity to the model that might generate new oscillations.

The model

I considered three species competing for three essential abiotic resources that were required for growth, i.e., nitrogen (N), phosphorus (P), and silica (Si). In this model, I assumed that each species had the highest requirement for one resource, and the specific growth rate of a species was determined by the resource that was most limiting as in Von Liebig's (1840) "Law of the Minimum".

I assumed that the specific growth rates were determined by the Droop's cell-quota equation (1973). Referring to equation (8), μ was the specific growth rate (d^{-1}), μ_{max} was the maximum specific growth rate (d^{-1}), Q_{min} was the minimum intracellular nutrient content required for survival of the algal cell (μmol $cell^{-1}$), and Q was the cell-quota (μmol $cell^{-1}$).

Michelis-Menten kinetics (Dugdale 1967) were used to describe the relationship between the nutrient uptake rate and ambient nutrient concentration:

$$\rho = \rho_{max}\left(\frac{S}{S + k_s}\right) \tag{9}$$

where ρ was the nutrient uptake rate (μmol $cell^{-1}$ d^{-1}), ρ_{max} was the maximum nutrient uptake rate (μmol $cell^{-1}$ d^{-1}), k_s was the half saturation constant for the nutrient uptake rate (μmol L^{-1}) and S was the dissolved nutrient concentration of the limiting nutrient (μmol L^{-1}).

The equations describing N uptake under N-limitation, P uptake under P-limitation, and Si uptake under Si-limiting conditions were

$$\rho_N = \rho_{maxN}\left(\frac{R_n}{R_n + k_N}\right) \quad (10)$$

$$\rho_P = \rho_{maxP}\left(\frac{R_p}{R_p + k_P}\right) \quad (11)$$

$$\rho_{Si} = \rho_{maxSi}\left(\frac{R_{si}}{R_{si} + k_{Si}}\right) \quad (12)$$

where ρ_N, ρ_P and ρ_{Si} were the N-uptake, P-uptake and Si-uptake rates (µmol cell^{-1} d^{-1}), respectively; ρ_{maxN}, ρ_{maxP} and ρ_{maxSi} were the maximum N-uptake, P-uptake and Si-uptake rates (µmol cell^{-1} d^{-1}), respectively; k_N, k_P and k_{Si} were the N, P and Si half saturation constant rates (µmol L^{-1}), respectively; and R_n, R_p and R_{si} were the ambient nitrogen, phosphorus and silica concentrations (µmol L^{-1}), respectively.

Uptake of P and Si under N-limiting conditions was a function of N-utilization, uptake of N and Si under P-limiting conditions was a function of P-utilization and uptake of N and P under Si-limiting conditions was a function of Si-utilization (Elrifi and Turpin 1986; Zonnevald 1996; Roelke et al. 1999). The following equations described P and Si uptake under N-limiting conditions:

$$\rho_P = \rho_{maxP}\left(\frac{R_p}{R_p + k_P}\right)\left(\frac{R_n}{R_n + a_N k_N}\right) \quad (13)$$

$$\rho_{Si} = \rho_{maxSi}\left(\frac{R_{si}}{R_{si} + k_{Si}}\right)\left(\frac{R_n}{R_n + a_N k_N}\right) \quad (14)$$

N and Si uptake under P-limiting conditions were described as follows:

$$\rho_N = \rho_{maxN}\left(\frac{R_n}{R_n + k_N}\right)\left(\frac{R_p}{R_p + a_P k_P}\right) \quad (15)$$

$$\rho_{Si} = \rho_{maxSi}\left(\frac{R_{si}}{R_{si} + k_{Si}}\right)\left(\frac{R_p}{R_p + a_P k_P}\right) \quad (16)$$

N and P uptake under Si-limiting conditions were described as follows:

$$\rho_N = \rho_{maxN}\left(\frac{R_n}{R_n + k_N}\right)\left(\frac{R_{si}}{R_{si} + a_{Si} k_{Si}}\right) \quad (17)$$

$$\rho_P = \rho_{maxP}\left(\frac{R_p}{R_p + k_P}\right)\left(\frac{R_{si}}{R_{si} + a_{Si} k_{Si}}\right) \quad (18)$$

where ρ_N, ρ_P, ρ_{Si}, ρ_{maxN}, ρ_{maxP}, ρ_{maxSi}, k_N, k_P, k_{Si}, R_n, R_p and R_{si} were as previously described, and a_N, a_P and a_{Si} were scaling factors.

The ambient N, P and Si ratio was compared to the optimum N, P and Si (opt-N : P, opt-N : Si, opt-P : Si) ratio to determine the limiting conditions of each nutrient. Survival is not possible below the minimum intracellular concentration of the limiting nutrient (Q_{min}), therefore the transition point from limitation by one nutrient to limitation by the other was described using the equations below:

$$\text{opt} - \text{N} : \text{P} = \frac{Q_{minN}}{Q_{minP}} \quad (19)$$

$$\text{opt} - \text{N} : \text{Si} = \frac{Q_{minN}}{Q_{minSi}} \quad (20)$$

$$\text{opt} - \text{P} : \text{Si} = \frac{Q_{minP}}{Q_{minSi}} \quad (21)$$

where Q_{minN}, Q_{minP} and Q_{minSi} were the minimum intracellular N, P and Si contents required for survival of the algal cell (μmol cell^{-1}), respectively.

Individual species abundance was described using differential equations based on

cell growth and flow characteristics:

$$\frac{dA_i}{dt} = A_i\left[\mu_i\left(R_n, R_p, R_{si}\right) - D\right] \tag{22}$$

i = 1, 2, 3

Here A_i was the abundance of species i (cells L^{-1}), R_n (µmol-N L^{-1}), R_p (µmol-P L^{-1}), R_{si} (µmol-Si L^{-1}) were the availability of resources, μ_i was the specific growth rate of species i (d^{-1}), and D was the flushing rate (d^{-1}).

The dynamics of the resources depended on the ambient resource supply, amounts of resources consumed by species, and flow to and from the system.

$$\frac{dN}{dt} = D\left(S_n - R_n\right) - \sum_{i=1}^{j} A_i \rho_{Ni} \tag{23}$$

$$\frac{dP}{dt} = D\left(S_p - R_p\right) - \sum_{i=1}^{j} A_i \rho_{Pi} \tag{24}$$

$$\frac{dSi}{dt} = D\left(S_{si} - R_{si}\right) - \sum_{i=1}^{j} A_i \rho_{Sii} \tag{25}$$

where N, P, Si, D, A_i, R_n, R_p and R_{si} were as previously described, ρ_{Ni}, ρ_{Pi} and ρ_{Sii} were the N, P and Si-uptake rates for species i, S_n, S_p and S_{si} were the N, P and Si concentrations of the resource supply (µmol L^{-1}), respectively.

Cell-quota decreases with increasing growth rate (Droop 1973; Elrifi and Turpin 1985), therefore changes in the N, P and Si cell-quota for each species were described as follows:

$$\frac{dQ_{Ni}}{dt} = \rho_{Ni} - \mu_{Ni} Q_{Ni} \tag{26}$$

$$\frac{dQ_{Pi}}{dt} = \rho_{Pi} - \mu_{Pi} Q_{Pi} \quad (27)$$

$$\frac{dQ_{Sii}}{dt} = \rho_{Sii} - \mu_{Sii} Q_{Sii} \quad (28)$$

where all symbols were as previously described.

Model equations presented above were solved using a fourth-order Runge-Kutta procedure with a fixed time step of 0.001 d. Parameterization was done according to phytoplankton. Unless stated otherwise, for all species, $A_{ini} = 0.1$, $\mu_{max} = 1\ d^{-1}$, $\rho_{max} = 0.1 \times 10\text{-}6\ \mu mol\ cell^{-1}\ d^{-1}$, $D = 0.25\ d^{-1}$, and as = 0.01 and for all resources, S = R = 10 $\mu mol\ L^{-1}$. These values were chosen according to previously done chemostat experiments and they are within the range of typical phytoplankton (Tilman 1977; Tilman 1982; Elrifi and Turpin 1985; Grover 1997). Mortality was not taken into account, temperature and irradiance was assumed to be constant. Finally, nutrient loading was assumed to be continuous.

Results

For the purpose of this research, I tested the model prediction of Huisman and Weissing (2001b) in which three species compete for three abiotic resources using a resource-storage-based model. In their model prediction, they stated three scenarios. (1) Stable coexistence, where each species consumed most of the resource for which it had the highest requirement. (2) Species oscillations and chaos where each species consumed most of the resource for which it had the intermediate requirement. (3) Competitive exclusion, where each species consumed most of the resource for which it had the lowest

requirement.

For comparison sake, I assumed that each species has the highest requirement for one resource. In order to satisfy the conditions that resulted in the prediction above, k_s and Q_{min} values were arranged according to the resource requirements (R*) of the species. R* values were determined by running simulations for each species (i = 1, 2, 3) when limited by resource j. R* values for each species under each condition are given in Table 7. Simulation codes for one species and three species were given in Appendix A.

Table 7. R* values for each species for three abiotic resources under different resource requirement and consumption conditions.

	Highest requirement - Highest consumption			Intermediate requirement- Highest consumption			Lowest requirement- Highest consumption		
	Rn*	Rp*	Rsi*	Rn*	Rp*	Rsi*	Rn*	Rp*	Rsi*
Sp1	0.005	0.14	0.12	0.004	0.12	0.097	0.004	0.12	0.096
Sp2	0.12	0.005	0.14	0.097	0.004	0.12	0.096	0.004	0.12
Sp3	0.14	0.12	0.005	0.12	0.097	0.004	0.12	0.096	0.004

Under similar conditions, when specific growth rates were controlled by resource-storage-based cell quota equations, the model predicted that the system generated species oscillations in which each species consumed most of the resource for which it had the highest requirement (Fig. 20). The matrixes used to create Fig. 20 were as follows:

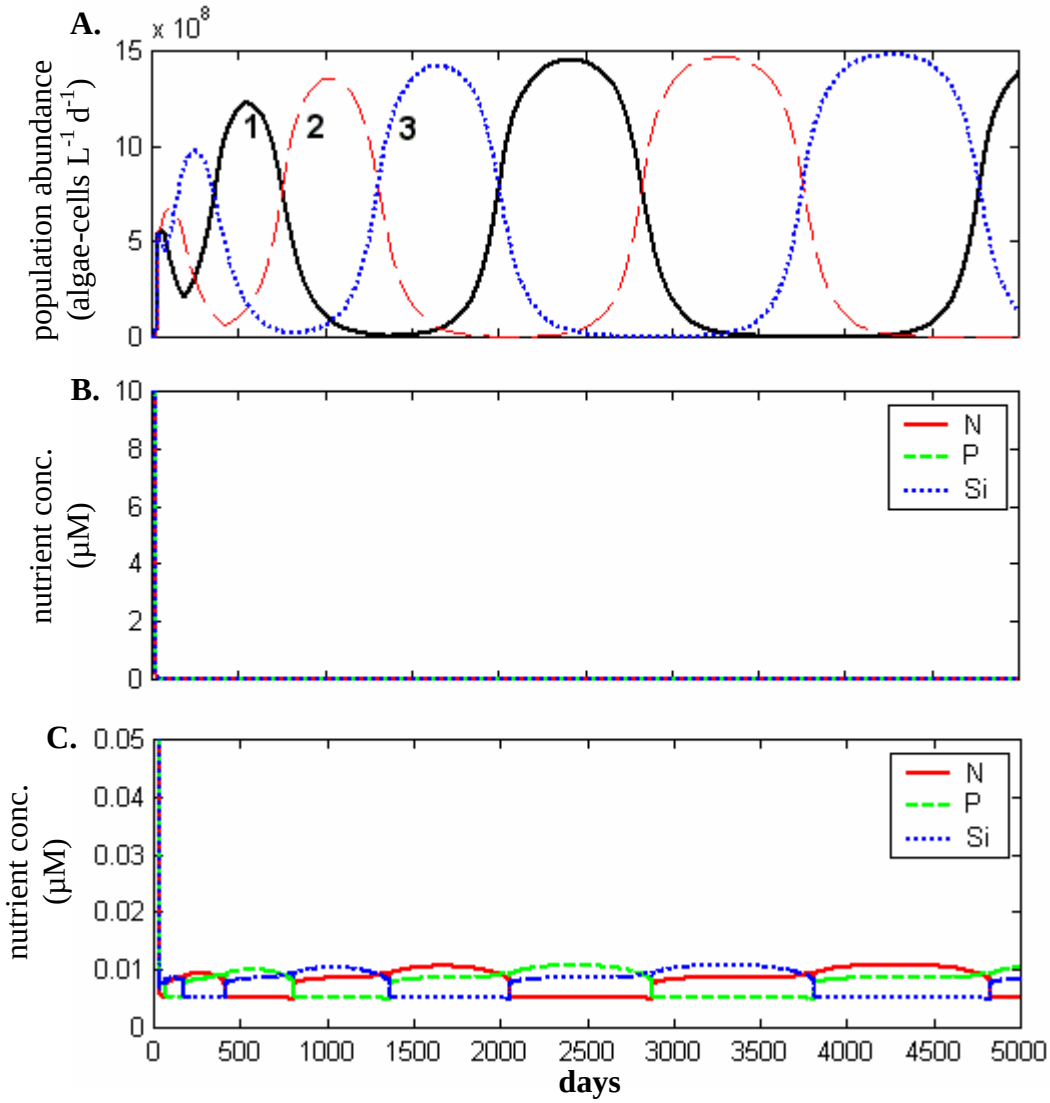

Fig. 20. Highest resource requirement-highest resource consumption generated species oscillations on three resources. (A) Population abundance of the three phytoplankton groups, (B) ambient nitrogen, phosphorus and silica concentrations, (C) close up to the ambient nitrogen, phosphorus and silica concentrations, (D) nitrogen, phosphorus and silica cell-quotas for three phytoplankton species, (E) close up to the nitrogen, phosphorus and silica cell-quotas for three phytoplankton species.

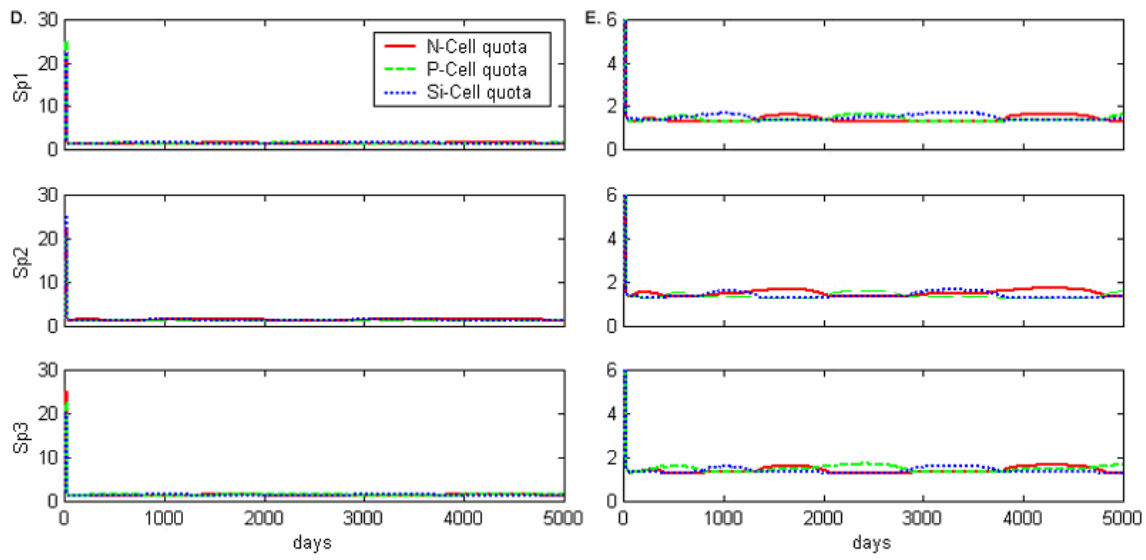

Fig. 20. Continued.

$$k_{ij} = \begin{bmatrix} 0.31 & 0.32 & 0.40 \\ 0.40 & 0.31 & 0.32 \\ 0.32 & 0.40 & 0.31 \end{bmatrix} \qquad Q_{\min ij} = \begin{bmatrix} 0.050 & 0.045 & 0.040 \\ 0.040 & 0.050 & 0.045 \\ 0.045 & 0.040 & 0.050 \end{bmatrix}$$

where i = Sp1, Sp2, Sp3 and j = N, P, Si.

When each species consumed most of the resource for which it had the intermediate requirement, competitive exclusion was observed (Fig. 21). The matrixes used to create Fig. 21 were as follows:

$$k_{ij} = \begin{bmatrix} 0.31 & 0.32 & 0.40 \\ 0.40 & 0.31 & 0.32 \\ 0.32 & 0.40 & 0.31 \end{bmatrix} \qquad Q_{\min ij} = \begin{bmatrix} 0.050 & 0.045 & 0.045 \\ 0.045 & 0.050 & 0.045 \\ 0.045 & 0.045 & 0.050 \end{bmatrix}$$

where all symbols were as previously described.

When each species consumed most of the resources for which it had the lowest requirement, the three species stably coexisted (Fig. 22). The matrixes used to create Fig. 22 were as follows:

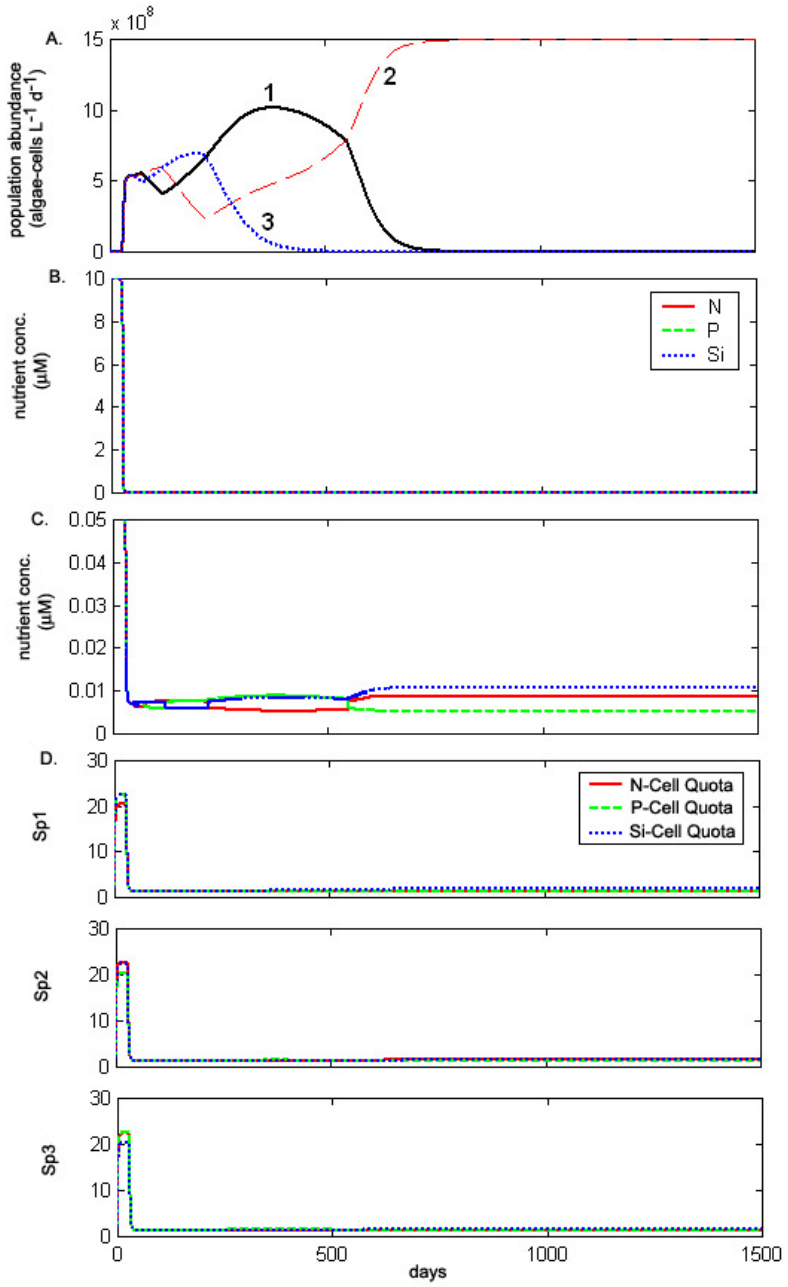

Fig. 21. Intermediate resource requirement-highest resource consumption generated competitive exclusion on three resources. (A) Population abundance of the three phytoplankton groups, (B) ambient nitrogen, phosphorus and silica concentrations, (C) close up to the ambient nitrogen, phosphorus and silica concentrations, (D) nitrogen, phosphorus and silica cell-quotas for three phytoplankton species.

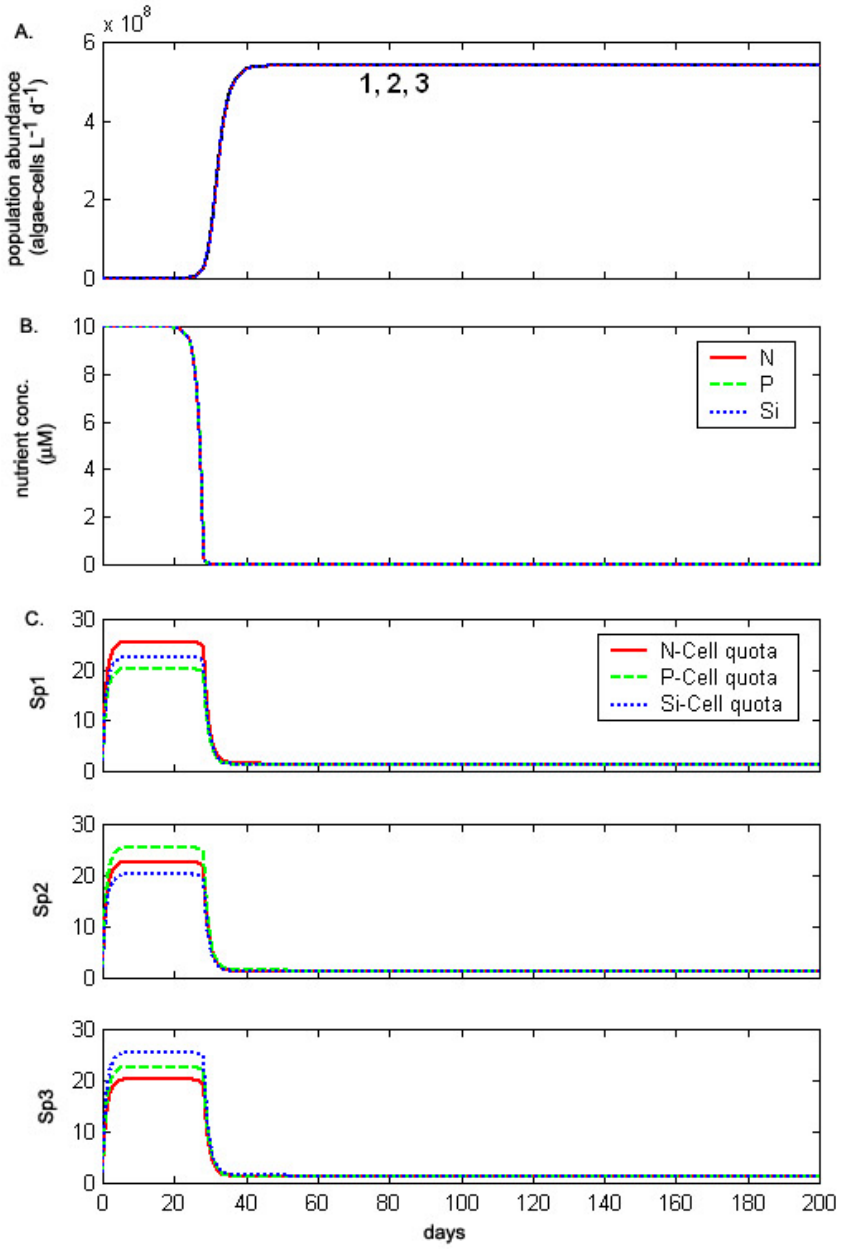

Fig. 22. Lowest resource requirement-highest resource consumption generated stable coexistence on three resources. (A) Population abundance of the three phytoplankton groups, (B) ambient nitrogen, phosphorus and silica concentrations, (C) nitrogen, phosphorus and silica cell-quotas for three phytoplankton species.

$$k_{ij} = \begin{vmatrix} 0.31 & 0.32 & 0.40 \\ 0.40 & 0.31 & 0.32 \\ 0.32 & 0.40 & 0.31 \end{vmatrix} \qquad Q_{\min ij} = \begin{vmatrix} 0.040 & 0.045 & 0.050 \\ 0.050 & 0.040 & 0.045 \\ 0.045 & 0.050 & 0.040 \end{vmatrix}$$

where all symbols were as previously described.

Sensitivity analysis

I performed a sensitivity analysis on the model to investigate how variations of the algal and system parameters influence the outcome of the competition. As a first step, initial conditions of each species (A_{ini}) were changed by either 0.005 or 0.05 increments for each condition. In this step, all other parameters were constant. The analysis was complete after initial conditions of each species or a combination of species for each condition was varied by different increments.

When each species consumed most of the resource for which it had the highest requirement, changing initial conditions did not change the overall outcome of the competition. However, which species would be the first to occur and the width of the periods of the heteroclinic cycle depended on the initial conditions (Fig. 23). Additionally, in some cases, accumulation of the biomass increased depending on the initial conditions.

When each species consumed most of the resource for which it had the intermediate requirement, changing initial conditions resulted in competitive exclusion where the winner depended on the initial conditions (Fig. 24). When each species consumed most of the resource for which it had the lowest requirement, changing initial conditions determined the steepness of the slope where each species reached the maximum biomass (Fig. 25). In addition, accumulated biomass spiked for a while then

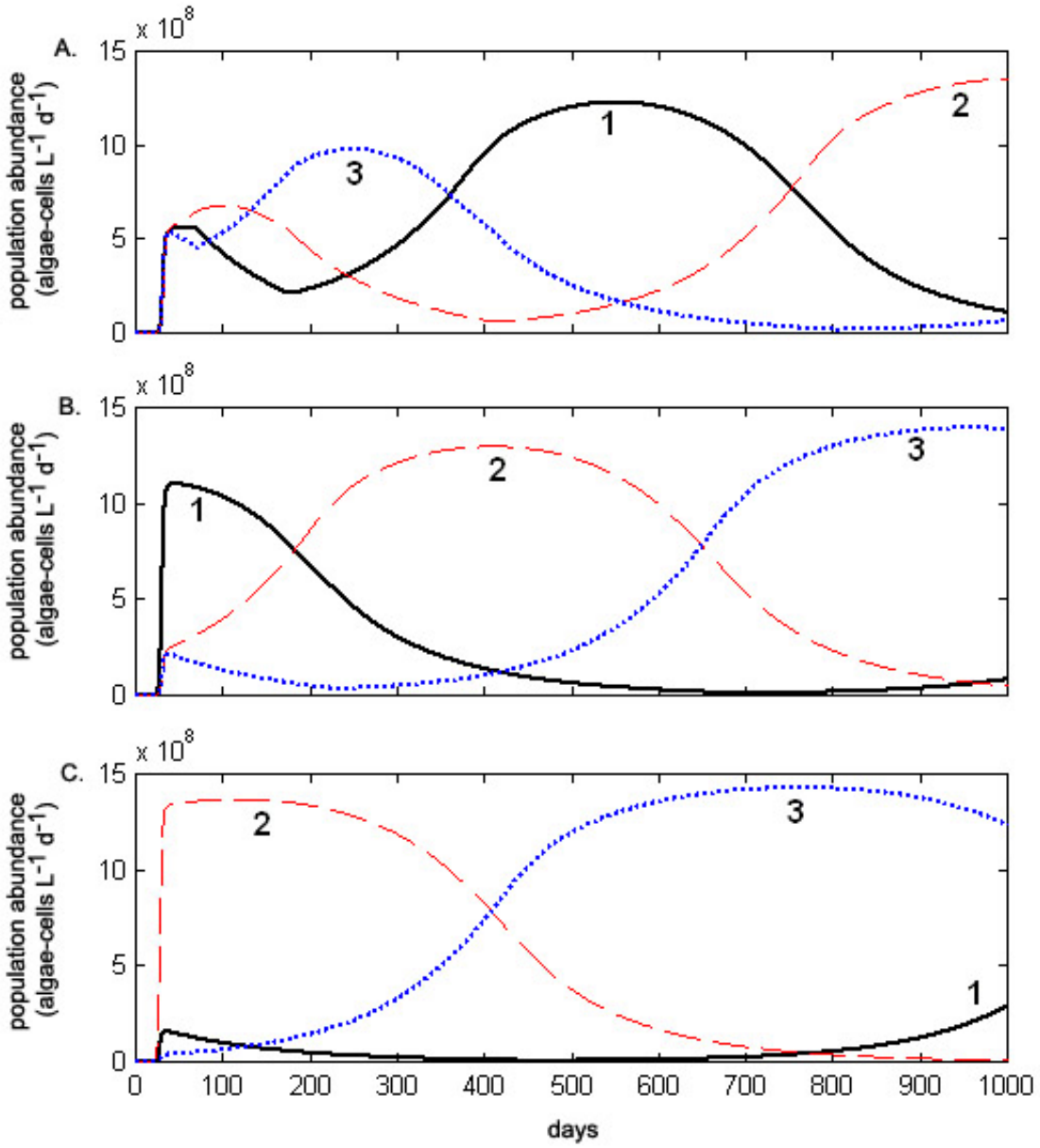

Fig. 23. Changing initial conditions generated heteroclinic cycles under highest resource requirement-highest resource consumption conditions. (A) A_{in} (Sp1, Sp2, Sp3) = 0.1, (B) A_{in} (Sp1) = 0.4 and A_{in} (Sp2, Sp3) = 0.1, (C) A_{in} (Sp1) = 0.4, A_{in} (Sp2) = 4.05, and A_{in} (Sp3) = 0.1.

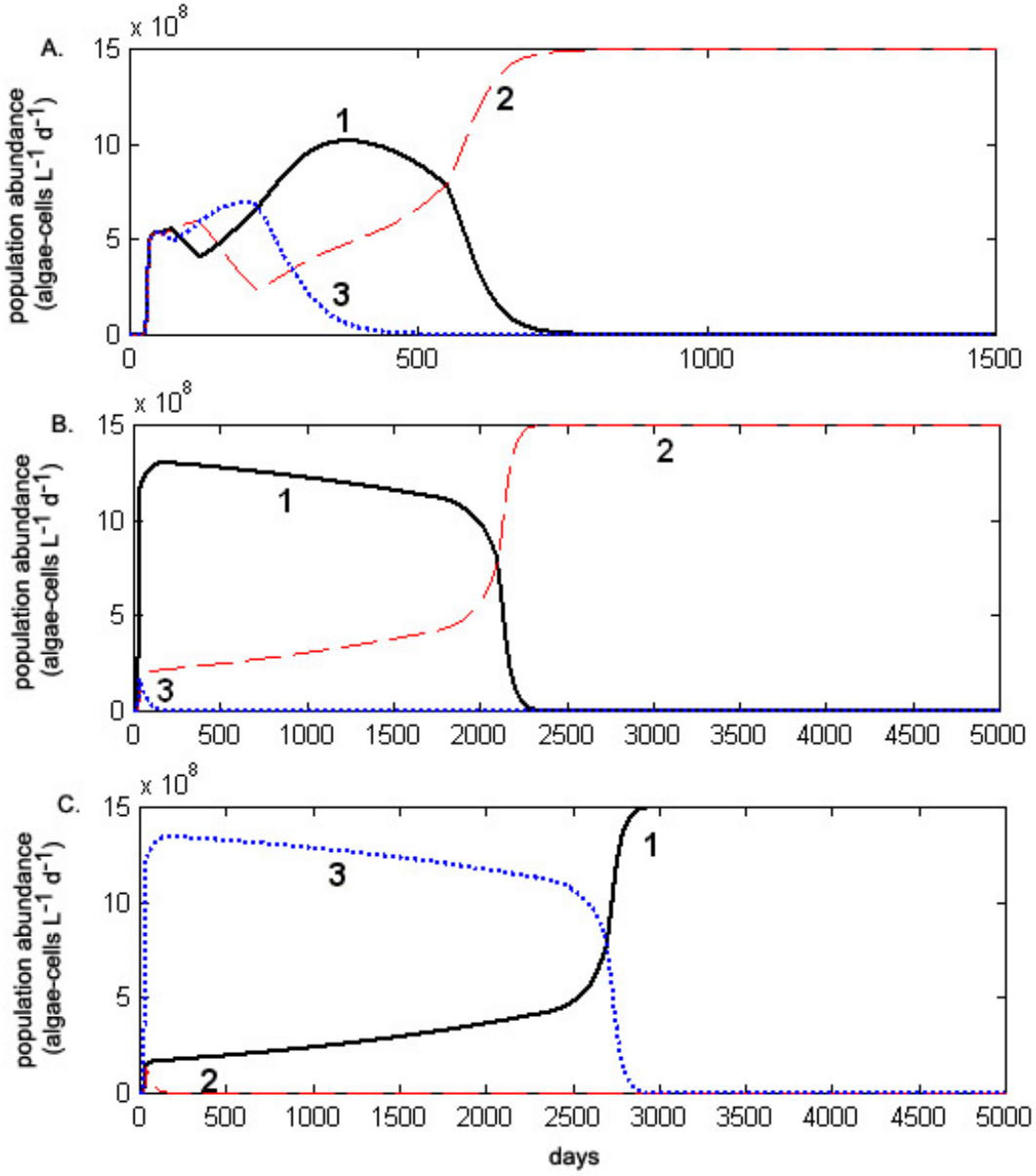

Fig. 24. The winner depended on the initial conditions under intermediate resource requirement-highest resource consumption conditions. (A) A_{in} (Sp1, Sp2, Sp3) = 0.1, (B) A_{in} (Sp1) = 0.8 and A_{in} (Sp2) = 0.4 and A_{in} (Sp3) = 0.1, (C) A_{in} (Sp1, Sp2) = 0.1and A_{in} (Sp3) = 0.8.

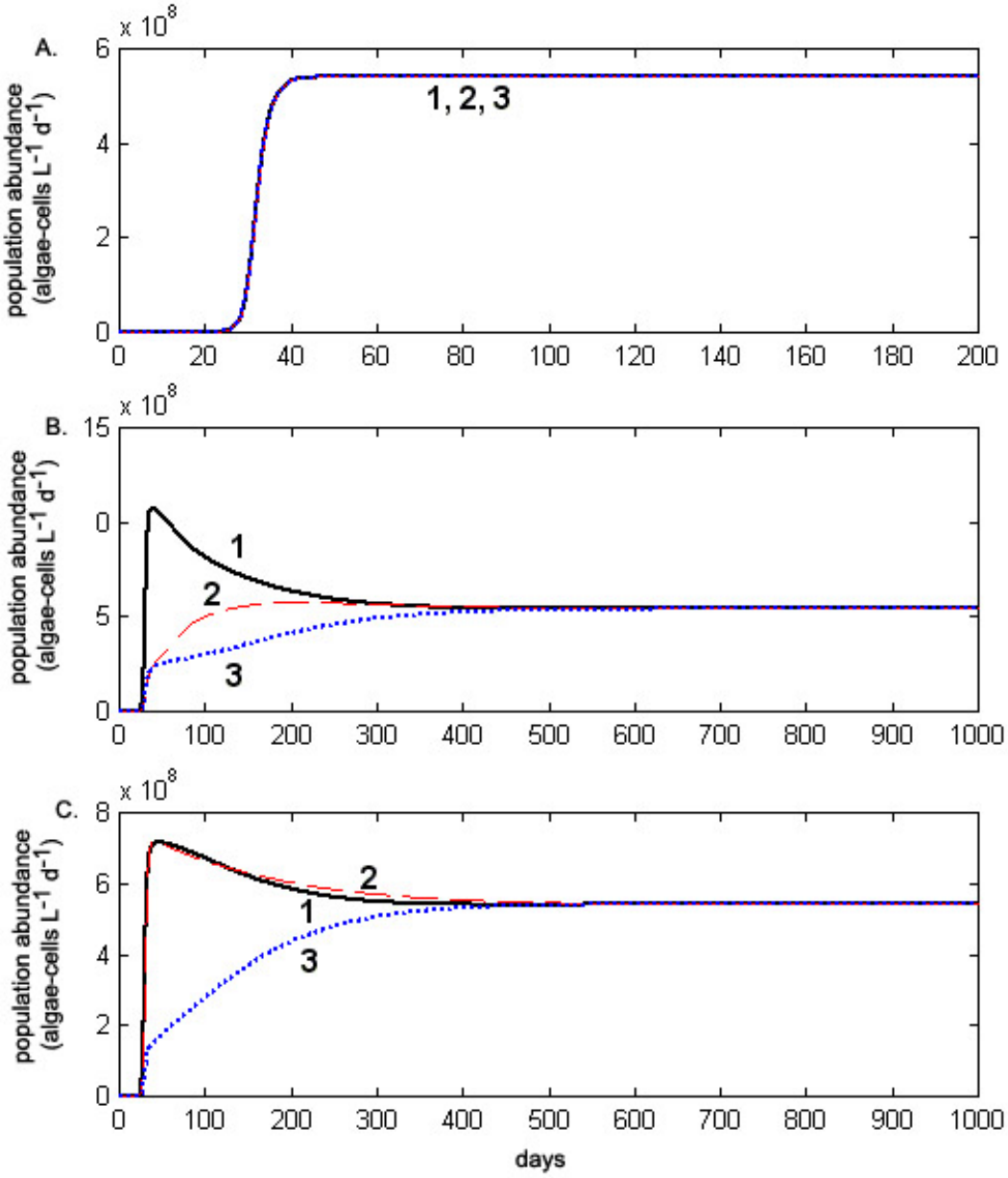

Fig. 25. Changing initial conditions changed the steepness of the slope where each species reached their maximum biomass under lowest resource requirement-highest resource consumption conditions. (A) A_{in} (Sp1, Sp2, Sp3) = 0.1, (B) A_{in} (Sp1) = 0.4 and A_{in} (Sp2, Sp3) = 0.1, (C) A_{in} (Sp1) = 0.4, A_{in} (Sp2) = 4.05, and A_{in} (Sp3) = 0.1.

reduced to the amounts that were observed when each species had the same initial conditions.

The second step in the sensitivity analysis was to change the concentrations of the nutrient supplies. In this step every other parameter was constant. Increasing the concentrations of two of the nutrient supplies resulted in competitive exclusion under the conditions of highest requirement-highest consumption (Fig. 26) and intermediate requirement-highest consumption (Fig. 27). The winner depended on the limiting nutrient and under which condition it was limited. Increasing the concentrations of two of the nutrient supplies resulted in stable coexistence of two species under the conditions of lowest requirement-highest consumption (Fig. 28). Species coexisting depended on the limiting nutrient and the conditions in which it was limited. For each condition, increasing the concentration of one of the nutrient supplies resulted in competitive exclusion. The winner depended on the non-limiting nutrient (Fig. 29) and the conditions in which it was non-limited (Fig. 30).

Discussion

I have shown that based on competition for abiotic resources, for certain species combinations a resource-storage-based model can generate chaotic oscillations in the form of heteroclinic cycles. Because of the sensitive dependence of species composition on initial conditions, the hallmark signature of chaos, divergence of nearby trajectories was also observed. My results confirmed previous findings of resource-storage-based models, which predicted dissimilar conditions of competition than models without

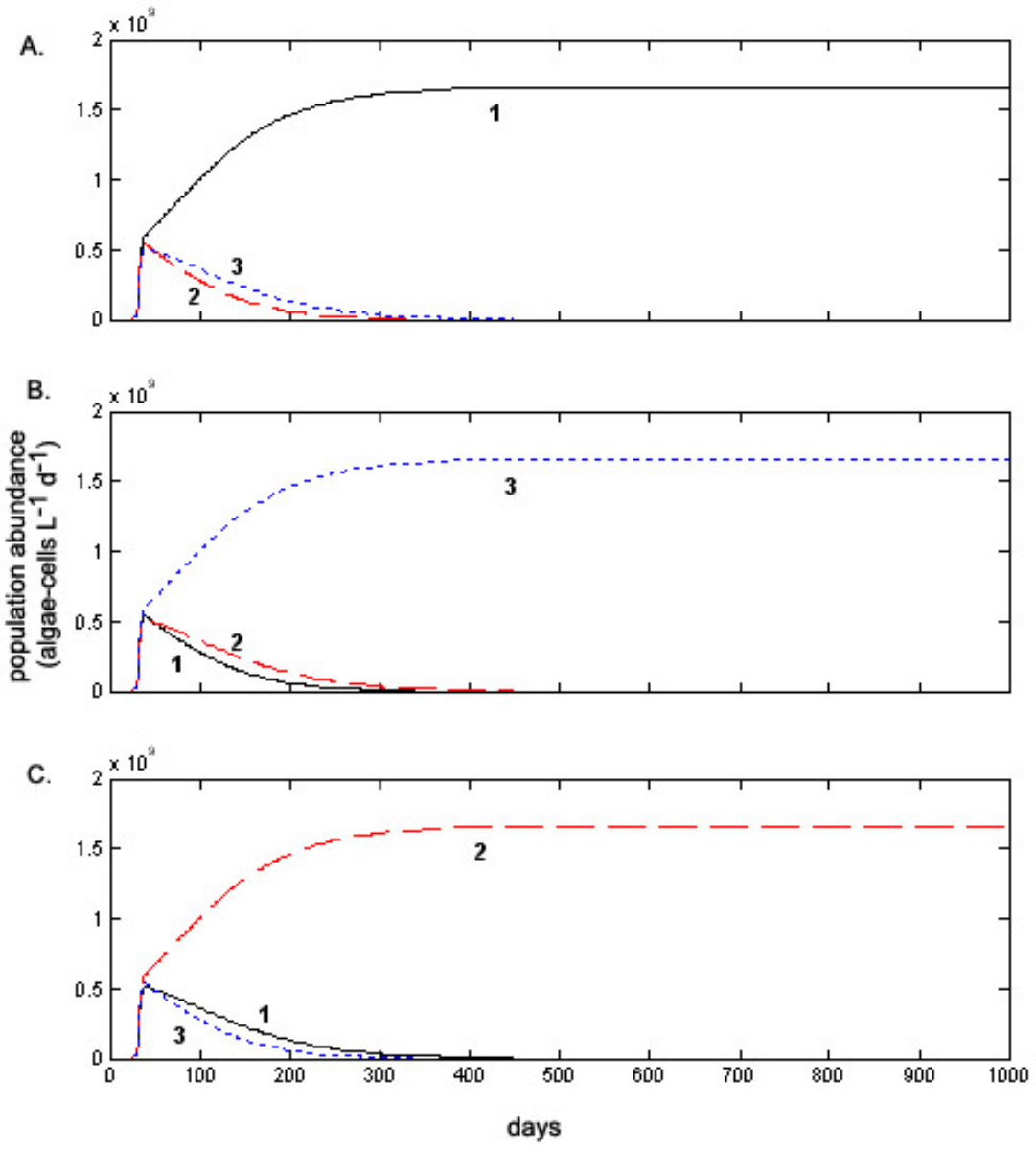

Fig. 26. Limitation by one of the resources caused competitive exclusion under highest resource requirement-highest resource consumption conditions. (A) S_n = 12 µmol L^{-1} and $S_p = S_{si}$ = 10 µmol L^{-1}, (B) S_p = 12 µmol L^{-1} and $S_n = S_{si}$ = 10 µmol L^{-1}, (C) S_{si} = 12 µmol L^{-1} and $S_n = S_p$ = 10 µmol L^{-1}.

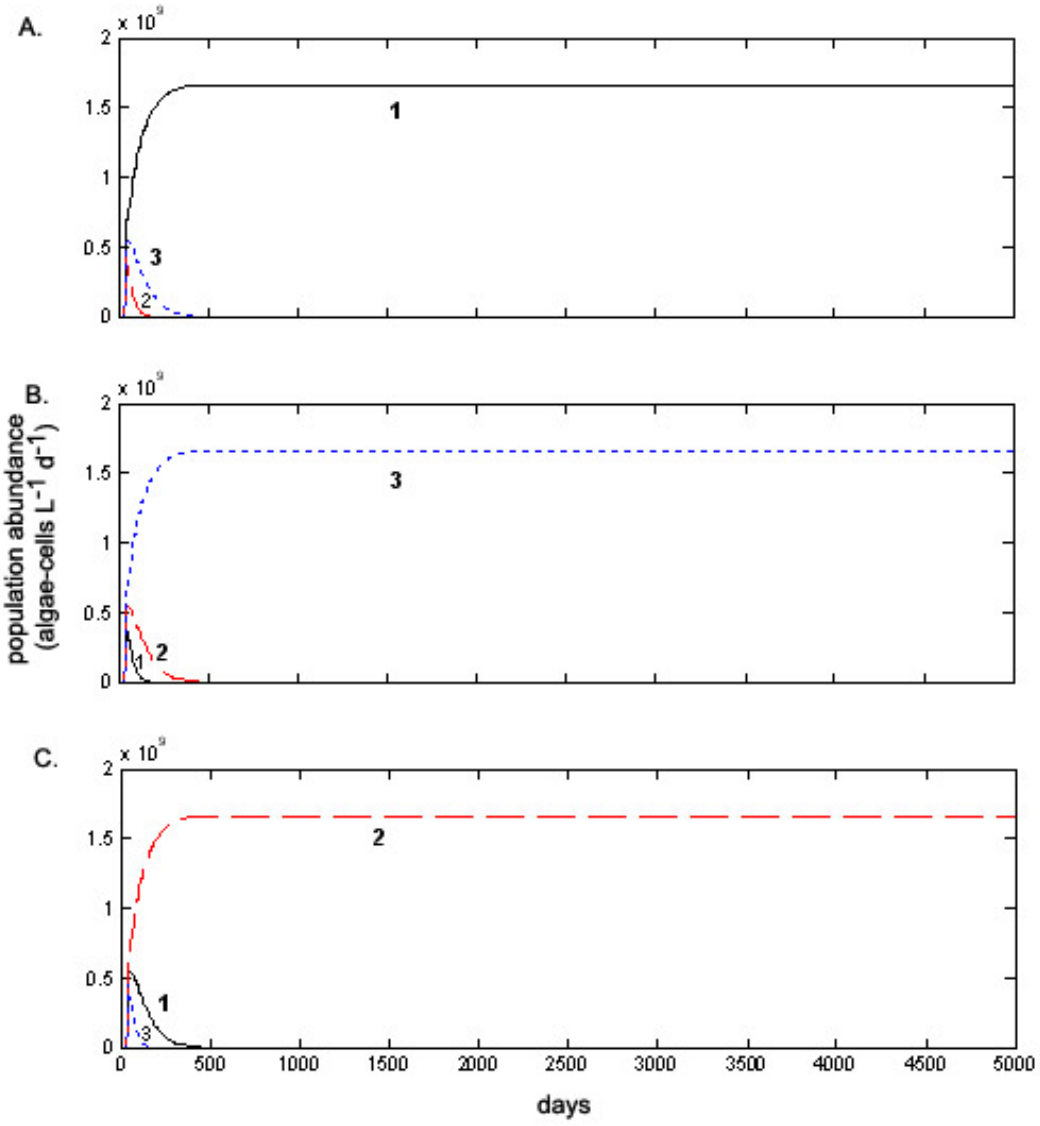

Fig. 27. Similar to the highest resource requirement-highest resource consumption condition, limitation by one of the resources caused competitive exclusion under intermediate resource requirement-highest resource consumption conditions. (A) S_n = 10 µmol L^{-1} and $S_p = S_{si}$ = 12 µmol L^{-1}, (B) S_p = 10 µmol L^{-1} and $S_n = S_{si}$ = 12 µmol L^{-1}, (C) S_{si} = 10 µmol L^{-1} and $S_n = S_p$ = 12 µmol L^{-1}.

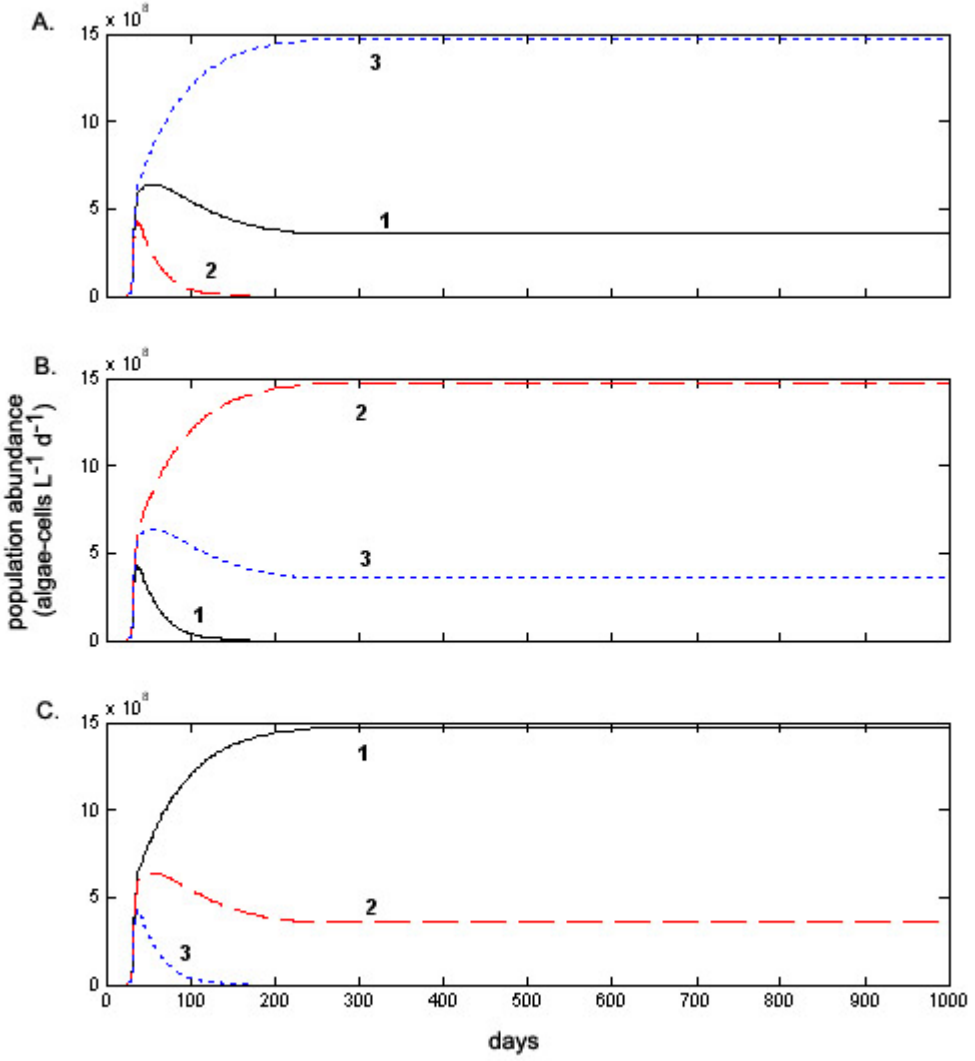

Fig. 28. Limitation by one of the resources caused stable coexistence of two species under lowest resource requirement-highest resource consumption conditions. (A) S_n = 10 µmol L^{-1} and $S_p = S_{si}$ = 12 µmol L^{-1}, (B) S_p = 10 µmol L^{-1} and $S_n = S_{si}$ = 12 µmol L^{-1}, (C) S_{si} = 10 µmol L^{-1} and $S_n = S_p$ = 12 µmol L^{-1}.

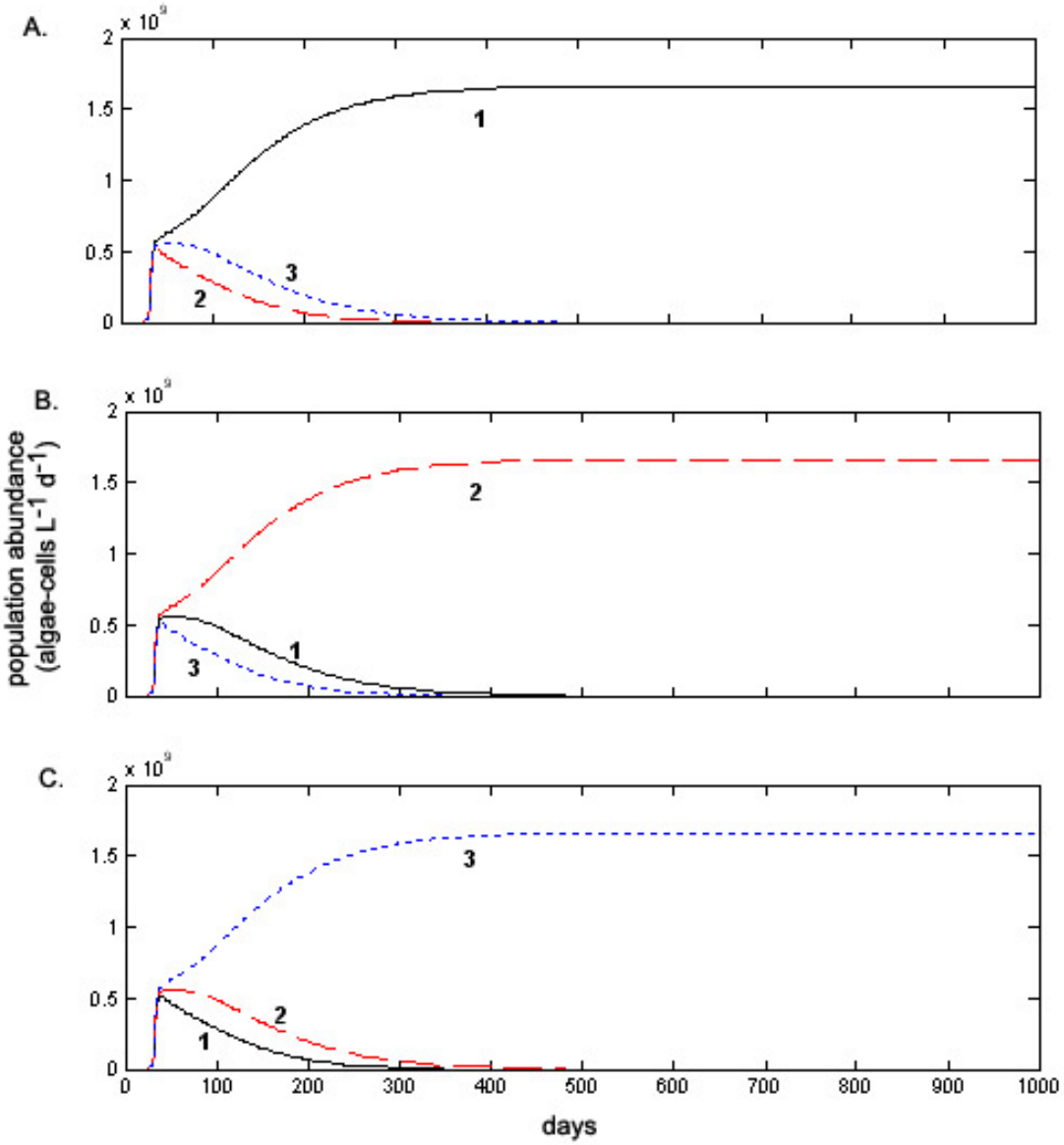

Fig. 29. Limitation by two of the resources caused competitive exclusion under all three conditions. This figure only shows the highest resource requirement-highest resource consumption condition. (A) S_n = 12 µmol L^{-1} and $S_p = S_{si}$ = 10 µmol L^{-1}, (B) S_p = 12 µmol L^{-1} and $S_n = S_{si}$ = 10 µmol L^{-1}, (C) S_{si} = 12 µmol L^{-1} and $S_n = S_p$ = 10 µmol L^{-1}.

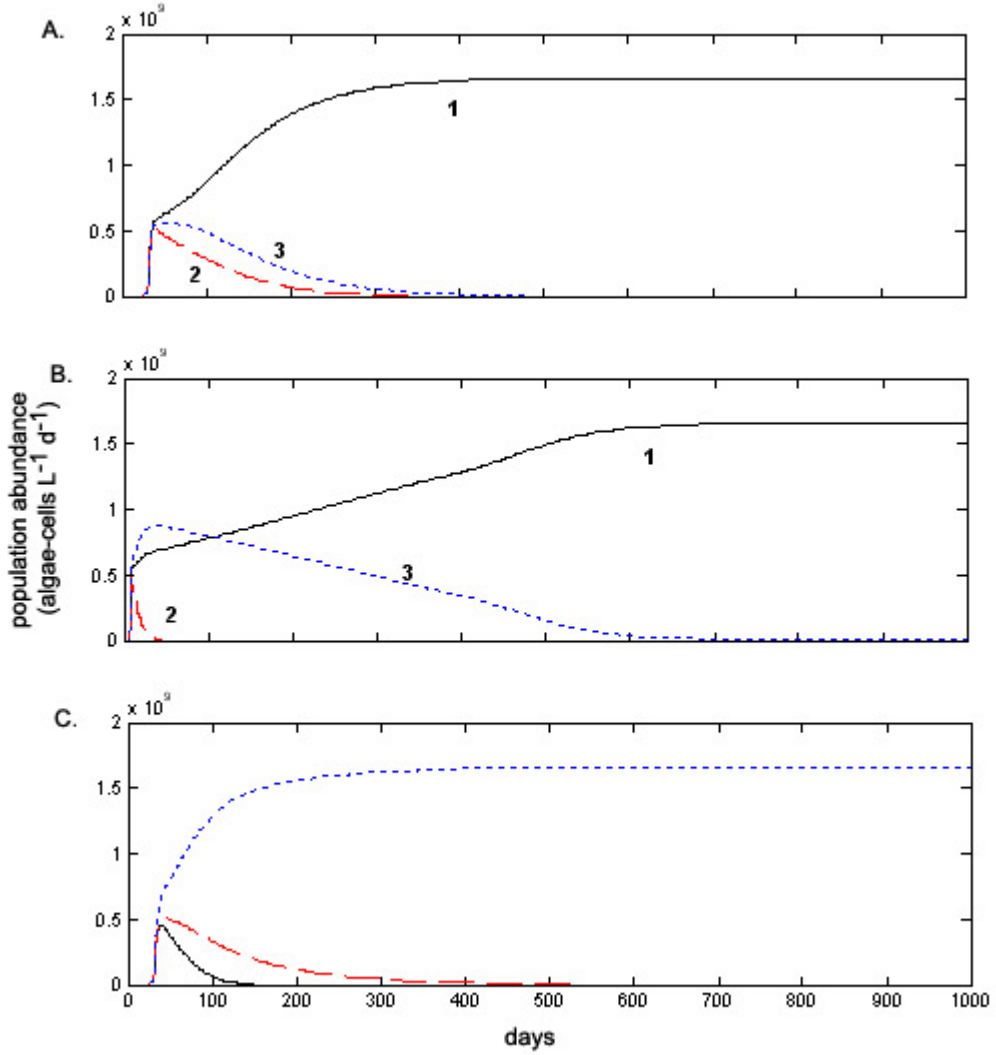

Fig. 30. The winner depended on the condition when two of the resources were limiting. This figure only shows S_n = 12 µmol L^{-1} and $S_p = S_{si}$ = 10 µmol L^{-1} for (A) highest resource requirement-highest resource consumption, (B) intermediate resource requirement-highest resource consumption, (C) lowest resource requirement-highest resource consumption.

resource storage (Grover 1990; Grover 1991a; Grover 1991b). Additionally, theoretical and experimental comparisons between two types of models have shown that storage-based models provide a better representation of competition under fluctuating conditions (Droop 1968; Droop 1983; Grover 1991b; Sommer 1991).

The highest requirement-highest consumption condition resulted in oscillations, which were in the form of heteroclinic cycles that gradually slowed down. Although the cycle periods became wider, the cyclic movement perpetuated indefinitely. Initial conditions determined the species that first occurred and periods of the heteroclinic cycle. For three species competing for three resources, heteroclinic cycles can be observed if the invasion is slower than the displacement of the focal species (Hutson and Law 1985; Huisman and Weissing 2001b) which was the case in this condition.

The intermediate requirement-highest consumption condition resulted in the competitive exclusion of species in which the initial conditions determined the winner. The time required for one species to out-compete the others was very long. The difference between the initial conditions for one species to displace the successor species was at least 8 fold. This occurred because the parameters that were used to satisfy this condition were very close to the parameters that were required for stable coexistence.

The lowest requirement-highest consumption condition resulted in the stable coexistence of three species in which the initial conditions determined the steepness of the slope where each species reached biomass maxima. The uptake of each nutrient under any nutrient limiting condition depended on the utilization of the other nutrients as well. Additionally, the ambient nutrient concentrations in the system changed depending

on the utilization by phytoplankton and flow to and from the system. Because the species that had the highest biomass has taken up the nutrients until they became limiting it had a steeper slope than the other two species.

When one of the nutrients was limiting, the species that had the lowest requirement for that limiting nutrient out-competed the other species under highest requirement-highest consumption and intermediate requirement-highest consumption conditions. Since competitive ability of a species for a resource depends on R* (Armstrong and McGehee 1980; Tilman 1982), the species with the lowest R* will win the competition.

Under lowest requirement-highest consumption conditions, the two species with the lowest and the intermediate R* for the limiting nutrient coexisted, while the species with the highest R* was displaced. This occurred because the species with the intermediate R* for the limiting nutrient also had the lowest R* for one of the non-limiting nutrients, and the species with the lowest R* for the limiting nutrient had the intermediate R* for the same non-limiting nutrient. Therefore, they were able to buffer the fluctuations caused by the limiting nutrient by internal storage of nutrients.

When two nutrients were limiting, the species that had the lowest R* for the non-limiting nutrient out-competed the other species under highest requirement-highest consumption and intermediate requirement-highest consumption conditions. This occurred because the species that had the lowest R* for the non-limiting nutrient also had the highest uptake rate for one of the limiting nutrients. In this manner, it was able to

store the limiting nutrient at a higher rate than the other two species and ultimately excluded them.

Under lowest requirement-highest consumption conditions, the species with the highest R* for the non-limiting nutrient out-competed the others. In this case this species had the lowest R* and highest uptake rate for one of the limiting nutrients. Therefore, it was able to uptake and store the limiting nutrient at a higher rate than the other two species. This way, again, it gained the advantage to exclude others.

The model was based on the assumptions that each species had the highest requirement for one resource and the specific growth rate of a species was determined by the resource that was most limiting as in Von Liebig's (1840) "Law of the Minimum". Although Huisman and Weissing (2001b) found that their predictions were not determined by this law, it would be interesting to see if this is true for the resource-storage-based models as well.

Nutrient loading was continuous in the model. A recent study by Roelke et al. (2003) showed that, in some cases, the mode of nutrient loading, i.e., pulsed vs. continuous, reduced oscillations created by competition and resulted in predictable outcomes. Therefore, another interesting study would be to investigate the effects of changes in nutrient loading mode in multi-species competition on resource-storage-based models.

Finally, nutrient uptake rates were constant for all species throughout the model simulations. Depending on the nutritional status of a cell, i. e., healthy, nutrient limited or starved, nutrient uptake rates can change (Lehman and Sandgren 1982; Riegman and

Mur 1984). Altering nutrient uptake rates may complicate interactions between consumers and their resources, which may generate additional non-linearity in the model or reduce the opportunities for oscillatory behavior.

CHAPTER VI

SUMMARY

In estuarine systems, it is important to allocate the limited freshwater resources effectively to maintain the ecological integrity of the marsh ecosystem. Therefore, one of the concerns of water resources managers is to determine the periodicity and magnitude of freshwater inflow that is necessary to sustain a functional connection between marsh vegetation, planktonic and benthic production as well as the production of commercially and recreationally important species, i. e., oysters, shrimp, fish and wildlife. Information gained from many studies indicated that, delivering freshwater inflow and nutrients in pulses may increase the quality of the phytoplankton species and alter the abundance of zooplankton accumulation. The increased quality of planktonic production may benefit the biological response of the marsh ecosystem in many ways, one of which is to stimulate the grazing food chain. Because planktonic productivity is a significant contributor to the total productivity , there is a link with higher trophic levels. Additionally, marsh areas provide important nursery habitats for many higher trophic level organisms, which may benefit from increased food and habitat quality. Because many commercially and recreationally important species graze on phytoplankton and zooplankton directly or indirectly, the focus of this study was the planktonic production.

Episodic inflow and nutrient loading events act as disturbances to aquatic systems, and often impact phytoplankton dynamics resulting in altered accumulated biomass, community structure, and species diversity. In turn, zooplankton populations

can be influenced. This hypothesis has been investigated theoretically. One of the resulting predictions was that pulsed inflow and nutrient loading would result in greater secondary productivity and less accumulated phytoplankton biomass compared to continuous inflow and nutrient loading. In this dissertation I tested this prediction through a series of semi-continuous design and flow-through incubation design experiments using natural plankton assemblages from a coastal estuary. I have also investigated the effects of resource-storage on multi-species competition of phytoplankton on multiple abiotic resources using a numerical model.

In this study, I showed that difference in flushing and nutrient loading mode altered zooplankton demographics, accumulation of phytoplankton biovolume, and phytoplankton species diversity. In all of the experiments, my results supported previous model predictions in which pulsed flushing and nutrient loading resulted in higher accumulation of grazer populations and phytoplankton species diversity. In addition, comparison of experiments of semi-continuous and flow-through design showed that pulsed inflows supported greater accumulation of some grazer populations and higher phytoplankton species diversity, when zooplankton were dominated by rotifers or by copepods. Deviations seen in phytoplankton biovolume were a result of the variations in initial phytoplankton community composition.

Findings from this study support the notion that resource managers must consider periodicity of flow along with magnitude of flow when considering landscape alterations and their impact on aquatic ecosystems. Nonetheless, depending on the target system and the dominant phytoplankton, chemostat experiments with trace metals i.e., iron, and

vitamins, i.e., Vit. B_{12}, might be necessary. In addition, experiments of the same nature must be conducted to investigate the effects of light limitation as well as the temperature differences. It may be that the distribution of light limits phytoplankton growth and development prior to consumption by organisms due to short day length, mixing, water transparency and/or self-shading by phytoplankton abundance. Similarly, temperature may have a secondary effect on the production processes affecting the salinity due to evaporation. Additionally, different phytoplankton are most competitive at different temperatures. Furthermore, experiments are needed to determine whether phytoplankton and zooplankton community would respond in a similar manner in the presence of non-selective grazers. Finally, further research must include in-field mesocosm experiments to verify these theoretical findings. This way, the complexity of the natural environment can better be replicated.

In one of my experiments, variability within the treatments and the difference of magnitude and the timing of the maximum phytoplankton biovolume, as well as the phytoplankton composition at the genera level was very high. Since understanding the mechanisms leading to high biodiversity are very important in predicting the winners of multi-species competition, inspired by this outcome, I decided to explore the effects of resource-storage on multi-species competition for three abiotic resources. Using a resource-storage-based numerical model, I demonstrated that for certain species combinations, resource-storage may lead to oscillations in the form of heteroclinic cycles. However, the proposed scheme of the model has some limitations.

First, in the model it has been assumed that each species had the highest requirement for one resource. Because co-limitation of some nutrients is possible, i.e., iron and nitrate, investigating the multiplicative effects of nutrients may be important. Second, nutrient supply was continuous. Supplying nutrients in pulses may complicate the nutrient-phytoplankton interaction and outcome of the competition may differ. Finally, nutrient uptake rates were assumed to be constant in the simulations. Nutrient uptake rates of phytoplankton may change depending on the nutrient status of the cells. Therefore, changing nutrient uptake rates may add additional non-linearity to the model, and will need further investigation.

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APPENDIX A

The following appendix contains a master program, a simulink model and differential solver function and a helper plotting function that was used to test a resource storage based competition model described in Chapter V.

```
%--------------------------------------------------------------------------
%  The master program for the simulations
%  File: runsimulation.m
%--------------------------------------------------------------------------
% Clear the Matlab Workspace before proceeding
clear;

% The following variables are shared between all files:
% - Master program
% - Simulink model
% - Function file
% - Plotting function
% thus are declared as globals
global umax m D aS Sn Sp Ssi kn kp ksi
global QminN QminP QminSi optNP optNSi optPSi pmaxN pmaxP pmaxSi

%--------------------------------------------------------------------------
% MODEL BEHAVIOUR
%--------------------------------------------------------------------------
% Define the behaviour of the model
% Set to 1 for multiple runs
REPEAT = 1;

if(REPEAT)
   % Define the Number of Runs, Note: varies according to simulation
   NUMBER_OF_RUNS = 41;
end

%--------------------------------------------------------------------------
% CONSTANTS
%--------------------------------------------------------------------------
umax = 1;      % Maximum specific growth rate (Day^-1)
m    = 0;      % Mortality rate (Day^-1)
D    = 0.25;   % Flushing rate (Day^-1)
aS   = 0.01;   % Scaling factor for uptake of non-limiting nutrients

% Resources (umole L^-1)
% Note: These may vary for each run.
Sn   = 10;
Sp   = 10;
Ssi  = 10;
```

```
% Values for half saturation indexes (umole L^-1)
% Note: These may vary for each run.
kn  = [0.31 0.32 0.40];
kp  = [0.40 0.31 0.32];
ksi = [0.32 0.40 0.31];

% Critical cell quota for different nutrients for species
% umole L^-1 Cell^-1)
% Note: These may vary for each run.
QminN  = [0.05e-7 0.045e-7 0.045e-7];
QminP  = [0.045e-7 0.05e-7 0.045e-7];
QminSi = [0.045e-7 0.045e-7 0.05e-7];

% Maximum nutrient uptake rate for species
% (umole Nutrient Cell^-1 Day^-1)
pmaxN  = [0.10e-6 0.10e-6 0.10e-6];
pmaxP  = [0.10e-6 0.10e-6 0.10e-6];
pmaxSi = [0.10e-6 0.10e-6 0.10e-6];

% Initial phytoplankton population size for each species
% (Cells L^-1)
Ain = [0.1 0.1 0.1];

%-------------------------------------------------------------------------
% Optimum resource ratio to determine the limiting conditions of each
% nutrient
optNP  = QminN./QminP;
optNSi = QminN./QminSi;
optPSi = QminP./QminSi;

% Initial nutrient concentrations (umole Nutrient)
Qnin  = 2*QminN;
Qpin  = 2*QminP;
Qsiin = 2*QminSi;

% Ambient nutrient concentration (umole L^-1)
Rn  = Sn;
Rp  = Sp;
Rsi = Ssi;

% Create the input for Matlab's differential solver
zin = [Ain, Qnin, Qpin, Qsiin, Rn, Rp, Rsi];

%-------------------------------------------------------------------------
if(REPEAT)
   %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
   % LOOP N TIMES WITH DIFFERENT Ain VALUES %
   %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
   for I=1:NUMBER_OF_RUNS,
      I=1;              % Show run number on screen

      % Run the Model in Simulink (Fig. 31)
      sim FixedStepSolver;
```

```
      % Create a filename and append the run number
      filename = sprintf('simout%d',I);

      % Save the Results (simout) of the Run to file
      save(filename,'simout');

      % Change the initial population sizes
      % Increment Ain, Note: May vary according to simulation
      Ain(1) = Ain(1) + 0.005;
      Ain(4) = Ain(4) + 0.05;

      % Create the Input for the Next Run
      zin = [Ain,Qnin,Qpin,Qsiin,Rn,Rp,Rsi];

      % Clear the last results store in the workspace
      clear simout;
   end
   %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
   % END OF LOOP                                   %
   %%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
else
   % Run the Model in Simulink
   % Note: To run the model faster in Matlab
   % for single runs, the data up to Zin may be copy
   % pasted into the Matlab workspace and the simulink
   % model may be run by pressing the run button from the simulink
   % window.  This also allows the user to see the time increments as
   % the model is running and also to pause the model if required.
   sim FixedStepSolver;

   % Create a filename and append the run number
   filename = sprintf('simout%d', 1);

   % Save the Results (simout) of the Run to file
   save(filename,'simout');
end
%-------------------------------------------------------------------------
```

```
%-------------------------------------------------------------------------
%  The function that the Matlab differential solver will use to solve
%  the equations
%  File: cellfunc.m
%-------------------------------------------------------------------------
function zdot = cellfunc(t,z);

% Same global variables have to be declared here as well as the main
% program
global umax m D aS Sn Sp Ssi kn kp ksi
global QminN QminP QminSi optNP optNSi optPSi pmaxN pmaxP pmaxSi

%-------------------------------------------------------------------------
% Retrieve the Data from the passed parameter z
A   = z(1:3)';
Qn  = z(4:6)';
Qp  = z(7:9)';
Qsi = z(10:12)';
Rn  = z(13);
Rp  = z(14);
Rsi = z(15);

% Limit the Qx so that it does not fall < QminX
for i=1:3,
   if Qn(i) < QminN(i),
      Qn(i) = QminN(i);
   end

   if Qp(i) < QminP(i),
      Qp(i) = QminP(i);
   end

   if Qsi(i) < QminSi(i),
      Qsi(i) = QminSi(i);
   end
end

% Part of droop equation
droopN  = (1 - QminN) ./ Qn;
droopP  = (1 - QminP) ./ Qp;
droopSi = (1 - QminSi)./ Qsi;

% Calculate specific growth rate, Invoke law of minimum
u = umax*min([droopN;droopP;droopSi]);

% Make sure values > 0
if Rn<0
   Rn  = 0;
end

if Rp<0
   Rp  = 0;
end
```

```
if Rsi<0
   Rsi = 0;
end

% Part of dugdale equation
dugdaleN = Rn  ./ (Rn+kn);
dugdaleP = Rp  ./ (Rp+kp);
dugdaleSi= Rsi ./ (Rsi+ksi);

% Determination of nutrient limiting conditions
for i=1:3
   if( ((Qn(i)/Qp(i)) < optNP(i)) & ((Qn(i)/Qsi(i)) < optNSi(i)) )
      % N limited uptake
      pn(i)  = pmaxN(i)  * dugdaleN(i);
      pp(i)  = pmaxP(i)  * dugdaleP(i)  * (Rn/(Rn+aS*kn(i)));
      psi(i) = pmaxSi(i) * dugdaleSi(i) * (Rn/(Rn+aS*kn(i)));
   elseif((Qp(i)/Qsi(i)) < optPSi(i))
      % P limited uptake
      pn(i)  = pmaxN(i)  * dugdaleN(i)  * (Rp/(Rp+aS*kp(i)));
      pp(i)  = pmaxP(i)  * dugdaleP(i);
      psi(i) = pmaxSi(i) * dugdaleSi(i) * (Rp/(Rp+aS*kp(i)));
   else
      % Si limited uptake
      pn(i)  = pmaxN(i)  * dugdaleN(i)  * (Rsi/(Rsi+aS*ksi(i)));
      pp(i)  = pmaxP(i)  * dugdaleP(i)  * (Rsi/(Rsi+aS*ksi(i)));
      psi(i) = pmaxSi(i) * dugdaleSi(i);
   end
end

% Algae nutrient uptake
AupN  = sum( A .* pn);
AupP  = sum( A .* pp);
AupSi = sum( A .* psi);

% Algae growth
Adot = A .* (u - m - D);

% Prepare output values
QNdot  = pn - Qn .* u;
QPdot  = pp - Qp .* u;
QSidot = psi - Qsi .* u;
Ndot   = D * (Sn-Rn) - AupN;
Pdot   = D * (Sp-Rp) - AupP;
Sidot  = D * (Ssi-Rsi) - AupSi;

% Output for the next iteration
zdot = [Adot,QNdot,QPdot,QSidot,Ndot,Pdot,Sidot]';
```

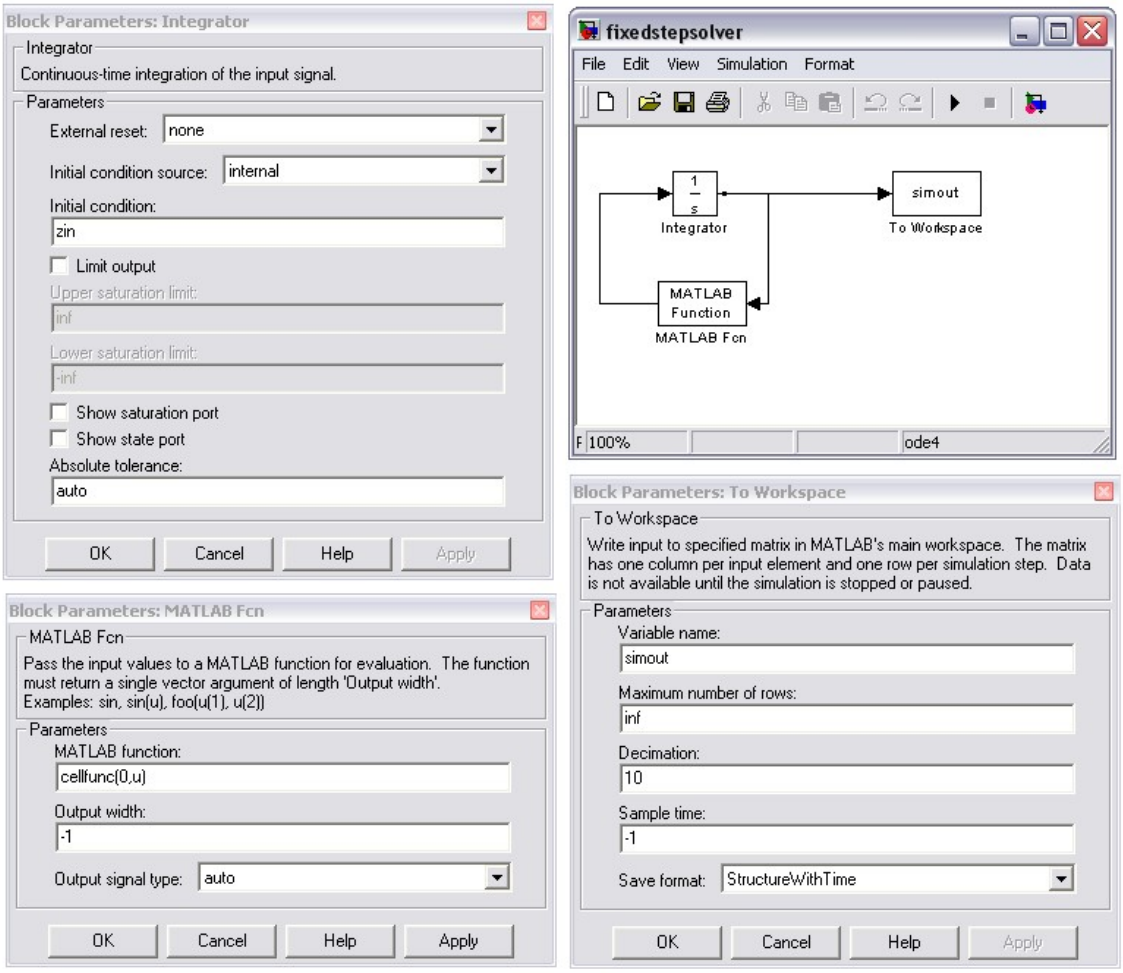

Fig. 31. Screen capture of the Simulink model used to solve the differential equations in the master program.

```
%-------------------------------------------------------------------------
%  The function that is used to plot the results of simulations
%  File: cellfunc.m
%-------------------------------------------------------------------------
function plotresults(plotnumber)

% Same global variables have to be declared here as well as the main
% program
global umax m D aS Sn Sp Ssi kn kp ksi
global QminN QminP QminSi optNP optNSi optPSi pmaxN pmaxP pmaxSi

% Load the file that was saved in the main program
filename = sprintf('simout%d',plotnumber);
load(filename);

% Simout is a structure that conbtains the time and data from the
% simulink run
% Retrieve the time and data from the simout variable
t = simout.time;
z = simout.signals.values;

% Plot the results
% Note, may vary according to simulation
figure

subplot(2,1,1);
plot(t,z(:,1),'k',t,z(:,2),'r',t,z(:,3),'b');
title('sp1-black, sp2-red, sp3-blue');
ylabel('algae-cells/l/d');

subplot(2,1,2);
hold on;
plot(t,z(:,13),'r');
plot(t,z(:,14),'g');
plot(t,z(:,15),'b');
title('N-red, P-green, Si-blue');
ylabel('uM');

figure
subplot(3,1,1);
hold on;
plot(t,z(:,4)./QminN(1),'r');
plot(t,z(:,7)./QminP(1),'g');
plot(t,z(:,10)./QminSi(1),'b');
ylabel('species 1');
title('Cell-Quota / N-red, P-green, Si-blue');

subplot(3,1,2);
hold on;
plot(t,z(:,5)./QminN(2),'r');
plot(t,z(:,8)./QminP(2),'g');
plot(t,z(:,11)./QminSi(2),'b');
ylabel('species 2');
```

```
subplot(3,1,3);
hold on;
plot(t,z(:,6)./QminN(3),'r');
plot(t,z(:,9)./QminP(3),'g');
plot(t,z(:,12)./QminSi(3),'b');
ylabel('species 3');
xlabel ('days');
```

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Education

1998 M.S. Wildlife and Fisheries Sciences, Texas A&M University, TX

1994 B.S. Agriculture Engineering, Minor in Aquatic ecology, Ankara Univ., Turkey

Recent Publications

Roelke, D.L., Y. Buyukates, M. Williams, J. Jean. 2003. Interannual variability in the seasonal plankton succession of a shallow, warm-water lake. Hydrobiol. Accepted.

Roelke, D.L., S. Augustine, Y. Buyukates. 2003. Fundamental predictability in multispecies competition: The influence of large disturbance. Am. Nat. Accepted.

Roelke, D.L., and Y. Buyukates. 2002. Dynamics of phytoplankton succession coupled to species diversity as a system-level tool for study of *Microcystis* population dynamics in eutrophic lakes. Limnol. Oceanogr. 47: 1109-1118.

Buyukates, Y., Rawles, S. D., and D. M. Gatlin III. 2000. Phosphorus composition of various feedstuffs and apparent phosphorus availability to channel catfish (*Ictalurus punctatus*). N. Am. J. Aqua. 62: 184-188.

Memeberships/Societies

2002-P Texas Academy of Science

1997-P American Society of Limnology and Oceanography